THE PROBLEM OF ADAPTIVE COLORATION WITH SPECIAL REFERENCE TO THE ANURA.

C O N T E N T S.

PLATES - I-XXI.

PART I. THE PROBLEM OF CONCEALMENT, CHIEFLY AS ILLUSTRATED BY THE ANURIA, AND WITH REFERENCE TO A SPECIAL ASPECT OF DISRUPTIVE COLORATION.

In attempting to account for the various phenomena of protective resemblance, warning coloration, and mimicry, we have to consider two questions which are involved, namely, their function and their cause. In other words, we are faced with the problems: (1) to what extent are these resemblances of value to the organism in which they are exhibited, as a means of defence against natural enemies, and (2) how have the phenomena (which include, besides coloration, many classes of adaptation such as form and attitude, special instincts, etc.) been established in the course of evolution?

Now these questions, though in a sense quite distinct from one another, are yet closely interrelated, and the solution of the second must inevitably depend upon the answer to the first. It is, therefore, of the utmost importance, especially in view of the heated controversies which surround the subject, that we should have abundant data and information regarding the function in nature of these resemblances. For it is here that the evidence is so conflicting, and it is against this point that the storms of controversy beat as violently as upon the various theories adduced to account for the facts themselves.

In 1862 Bates published his famous memoir on mimicry in Amazonian butterflies (6) , to be followed within a few years by parallel discoveries in the Malay region by Wallace(127), by Trimen in South Africa (125), and by Müller (78). Bates's original theory of mimicry, and the explanation of warning coloration as proposed by Wallace, resting upon the assumption that these classes of colours are effectual as a means of defence against insectivorous animals, was based on evidence which amounted to little more than a few scattered observations. Since that time the subject has attracted a great deal of attention, and has undergone remarkable development. During the last fifty years an immense number of observations in the field and experiments on captive animals have been carried out in order to test the validity of the theories of mimicry and warning coloration. Meanwhile these theories have undergone considerable modification, and have been widely extended in their application. There is now devoted to the subject a very extensive and voluminous literature which it well deserves, for it is one of unusual interest, embracing, as it undoubtedly does, some of the most remarkable phenomena in the whole field of biology.

The great accumulation of facts and evidence which have been brought to light by the masterly work of such investigators as Marshall, Poulton, Swynnerton, Hale Carpenter, Morton Jones, Kluijver, and others, has done much to establish the view originally held by the pioneer naturalists - namely, that it is to natural selection that we must look for an explanation of the phenonmena - and to place the theories of warning coloration and mimicry on a foundation firmly laid on the evidence of experiment and observation.

On the other hand, it is clear that the accumulation of further reliable evidence regarding the protective value of animal coloration is greatly needed.

The bulk of our information, whether derived from field observations, experiments, or other sources, has been primarily concerned with insects considered in relation to the predatory attacks of other Arthropods and of birds and mammals. So far as I am aware, this is the first attempt that has been made (1) to study in detail the predatory habits of Anura as factors in the evolution of adaptive coloration in insects; and (2) to draw attention to the analogy between concealing and warning coloration in frogs and insects respectively. It is hoped that the observations which form the basis of the present thesis, in contributing to a knowledge of the ecology of frogs, - of their place in the animal community, their enemies, their feeding-habits and food preferences, - will both bring these enemies of insects into line with those other groups which have long been generally recognised as factors in the production of warning colours, mimcry and allied phenomena; and also extend the application of the theories of concealing and warning coloration to the frogs themselves.

In the present Part, a certain aspect of the problem of concealing coloration (chiefly as applied to the Anura) is discussed, - namely the manner in which concealment in nature is brought about.

I wish to emphasise at the outset an important point, namely that it is 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 enemies and prey.

The truth of this statement may be seen by comparing the hawk moth (Plate XVIII) seen in its natural surroundings with the same insect in a museum cabinet; or the toad (Plate XIV) crouching among leaves on the forest floor of its native habitat with a similar animal lying dead in a dish of alcohol (Plate XI).

In order to retain where possible the correlation between the appearance of the living animal and its natural surroundings, I have made full use of the camera. By this means it has been possible to bring home from the tropics of South America and East Africa not only specimens themselves, but - so to speak - a part of the surrounding environment as well. Reference is made here to the photographs on

Plates II, VII, VIII, IX, XIV, XV, XVI, XVII, XVIII and XIX, for it is believed that these will furnish a more convincing statement than could any verbal description, of the effectiveness of various types of concealment in nature.

1. The Methods by which Concealment is brought about.

The purpose of concealing coloration is deceive, by rendering an animal unrecognizable to enemies or to prey; its success depends upon the creation of optical illusions. The precise nature of these illusions, lies in the province of the artist rather than of the naturalist. Briefly, they depend upon the following classes of facts:- Form can only be visible when it is differentiated from its background, (a) by colour or tone, or (b) by light and shade. In the absence of varying colour, tone and shade visible form cannot exist.

It therefore follows from these considerations that the essential steps towards inconspicuousness must lie in the direction (a) of colour resemblance, - i.e. the agreement in colour between an object and the background against which it is seen; and (b) of obliterative shading (Thayer's principle), - i.e. counter lightening in tone and shading which abolishes the appearance of roundness or relief, caused by light and shade. To these must be added (c) the further important principle of disruptive colouring i.e. a superimposed pattern of contrasted colours or tones which serves effectively to break up real form, which is replaced by an apparent but unreal form, and which thus renders the object even more difficult to recognise.

These theoretical principles of colour resemblance, obliterative shading, and disruptive colouring, together with various additional devices which make for deception, are those actually found to operate in nature.

It frequently happens that an animal embodies two, or all three, of the above principles in its colour scheme. An example of the latter is *Rana temporaria* (Plate II.).

It would be out of place here to discuss further the general aspects of this subject. There is however a special aspect of disruptive coloration to which we must now refer.

2. Coincident disruptive coloration.

Disruptive coloration has for its purpose the making of the configuration proper to the body of an animal as weak as possible, by the superimposition of an alternative configuration, which, as we say "catches the eye". The strength of the superimposed pattern depends upon various factors, such as the size and shape of its component parts and the colour and/or tonal differentiation between adjacent parts.

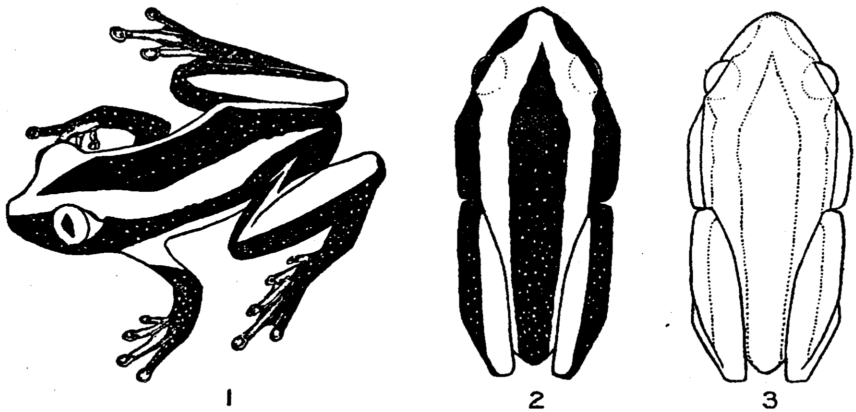
Now if we investigate disruptive patterns in relation to the characteristic habits of posture of the animals wearing them, it is found that in many animals the pattern-units, (such as bars or stripes of lighter or darker pigment), extend across separate, but adjacent parts of the body. The effect of this is greatly to strengthen the pattern in its effect on the beholder, for it unites the very parts of the body which are, in fact, separate entities.

My attention was first directed to this principle by the very remarkable and striking pattern of the tree frog *Megalixalus fornasinii* in East Africa (Plate VIII). When seen in the characteristic resting attitude, with the limbs closely applied to the sides of the body, it will be noticed that the broad and very conspicuous silvery dorsal stripes exactly coincide with similar stripes on the legs. The attitude, and the very striking colour scheme combine to produce an extraordinary effect, which, like the 'dazzle' painting of war time, tends to make the object look other than it really is. The deceptive appearance, brought about by a combined effect of pigment and posture, depends upon the breaking up of the body into two contrasting areas of brown and white. Considered separately, neither part resembles part of a frog. Together in nature the strong white region alone is conspicuous. This distracts an observer's attention

TABLE I.—The Predatory Habits of *M. fornasinii* in relation to those of other Tree-Frogs.

Stomachs examined.	Odonata.	Acridiidæ.	Muscidæ, etc.	Culicidæ, etc.	Lepidoptera.
M. fornasinii (360 frogs).	10	7	162	132	26
All other spp. (438 frogs).	2	4	35	27	11

Text-figure 1.



Megalixalus fornasinii. Drawn from photographs of living specimens, to illustrate the "disruptive" type of concealing coloration, which operates (No. 2) when the frog assumes its characteristic crouching posture. (See Pl. I. fig. 2.)

from the true form and contour of the body on which it is superimposed, and, like a veil obliterating the features of its wearer, effectively masks its identity.

Evidence of the value of this colour scheme in relation to the capture of insect prey has been discussed elsewhere (Cott, 20 and see Text-fig. 1 and Table I).

It is of considerable interest to note that in Brazil a totally unrelated tree frog, Hyla leucophyllata, wears an almost identical pattern, which likewise extends from the back to the thigh.

Moreover, the same principle is widely applicable to the Anura generally, for frogs, toads, and tree frogs belonging to many families and representing every geographical realm are found to wear patterns of the type under discussion. In some cases, as in the tree frog Rhacophorus fasciatus from Sarawak, the bands extend transversely across the back and onto the legs. However, the commonest case is that in which transverse leg-bands agree in width and position so that they appear to extend (when the leg is folded) unbroken across two, or across three, adjacent segments of the limb. (See Plates IV, VIII—XIII). The following are some species in which marked correlation of this type has been noted:- Ranidae:- Rana temporaria (Europe) R. ornatissima, R. adspersa (East Africa); Amphignathodontidae:- Amphignathodon guentheri (Ecuador); Rhacophoridae:- Kassina senegalensis (Africa);

Discoglossidae:- Discoglossus pictus (Sardinia); Ceratophryidae:- Hylodes ventrimaculatus (Ecuador), H. longirostris (Ecuador), Physalaemus gracilis (Tehuantepec), Edalorhina bucklei (Canelos), Eleutherodactylus ruthi (Dominica); Brevicipitidae:- Microhyla picta (China), Gastrophryne elegans (Cordova), Ramanella montana (Malabar); Phrynomeridae: Phrynomerus bifasciatus (Africa); Pelobatidae:- Batrachopsis megalopyga (New Guinea); Hylidae:- Hyla resenbergii (Ecuador), H. venulosa (Brazil) etc.; Bufonidae:- Bufo valliceps (Nicaragua), Bufo typhonius (Colombia, Ecuador, Brazil), Bufo ockendeni (Peru); Liopelmidae: Liopelma sp. (New Zealand).

It appears then that this principle of coincident disruptive coloration is widely applicable in the Anura. But further, it also occurs widely in other groups, and we may mention in passing that it is found in snakes such as Vipera superciliaris (Plate V), where the pattern above and below the jaw corresponds; in many fishes, where the extension is from the scales of the body to the fins; and very widely in insects, especially Lepidoptera, in many species of which there is a close parallelism with frogs in this connection (See part II). A specialization of the same principle is seen in relation to the eyes of many vertebrates - including fishes, newts and salamanders, frogs, lizards, snakes, birds and mammals - in which a dark band, generally the same width as the diameter of the pupil, extends from the pupil, across the iris (see Rana temporaria, Plate II) onto adjacent scales, skin, feathers (see Woodcock, Plate VII) or hair. In each case, the effect is the same, namely to strengthen the superimposed configuration, and to obliterate the (otherwise) conspicuous eye.

3. An Investigation of the Leg-pattern in Rana temporaria.

In a detailed investigation of this phenomenon in the case of the leg patterns of Rana temporaria, the number and position of transverse bands on the left legs of 300 frogs (187 males and 113 females) have been tabulated, particular attention being paid to the width and relative position of adjacent parts of the pattern.

Three dark transverse bands on each of the three leg-segments is the normal pattern formula. In such a leg there are six points where coincidence between adjacent bands may, or may not occur, i.e. three between thigh and shin, and three between shin and foot. Cases where four series of pigment-bands occur (which are rather unusual) raise the maximum coincidence number to eight.

The following are the main results of this investigation:- (1) Of the 300 legs examined, in only 31 was there no coincidence of pattern: coincidence at one point occurred in 59 legs; at two points in 73; at three points in 69; at four points in 44; at five points in 15; at six points in 6;

at seven points in 2; and at eight points in one individual. In 55 legs the correspondence of pattern was between thigh and shin; in 48 between shin and foot; and in 166 there was coincidence right across the three segments of the leg.

4. Special Protection Resemblances.

Before leaving the question of concealing coloration in the Anura, two further devices which render recognition by an enemy more difficult must be mentioned.

In the first place, several Anura, particularly South American Bufonids and certain Brevicipitids, possess conspicuous ocelli on the groins. Such eyelike markings are found in *Mantipus ocellatus*, *Eupemphix nattereri* (Plate X, fig. 2) and *Gastrophryne elegans* (Plate XII, fig. 1). These markings are somewhat similar in appearance and position to the ocelli on the wings of certain Lepidoptera, and it is possible that we have here a further example of the parallelism between the adaptive colouring of frogs and insects (See Part II).

Finally, certain frogs and tree frogs may be cited as affording examples of special protective resemblance similar to the resemblances so well known among Orthoptera, Lepidoptera and other insects. The case of a leaf-resembling toad has been described in detail elsewhere (Cott, 14), and it is of interest to compare the photographs of this animal and of the leaf-like Blood Vein moth, figured respectively on Plates

XIV and XV.

Many bark-dwelling tree frogs, such as Hyla squirella (Florida), and Chiromatis xerampelina (East Africa, Plate XVI) compare favourably with procryptic bark-resembling insects, such as the moth Xanthopan morgani morgani (East Africa, Plate XVIII), as very prefect examples concealing coloration.

PART II. THE PROTECTIVE ADAPTATIONS OF ANURA, WITH SPECIAL REFERENCE TO THE THEORY OF WARNING COLOURS.

1. The Analogy between Adaptive Coloration in Frogs and Insects.

The bulk of the work that has been published on the theories of concealing and warning coloration has been in reference to the Insecta, to which group these theories were first applied. The adaptive significance of colour in frogs has been little studied in the past.

When applied to the Anura, the facts at our disposal indicate very clearly that we have in these batrachians phenomena closely parallel to many of those relating to procryptic and aposematic colouring in insects.

In the present section we shall indicate briefly to what extent the various features of adaptive colouring in the latter group (Insecta) find their analogy here. Several aspects of this parallelism have already been considered, i.e. from the point of view of concealment (Part I), and need only be mentioned here in passing.

The following types of concealing coloration are common to, and more or less widely applicable to, both Insecta and Anura:

(1) General protective resemblance in many, and probably the majority of defenceless and relatively edible forms,

to the dominant colour scheme of the environment:- namely, earth-colour in terrestrial forms, as in many Acridiidae, in Lepidoptera (Vanessa cardui), and in Bufo spp.; green and brown - often in the form of disruptive patterns - in grass dwellers, as in Acrida sulphuripennis (Pl. XIX) and Rana temporaria (Pl. II); grey and bark-like in branch dwellers (see below); grey in rock-dwelling forms, such as Hyla arenicola; and leaf-green, as in many tree-dwelling Hemiptera, Orthoptera, Lepidoptera and in many tree frogs (Hyla caerulia, H. andersoni, Leptopelis johnstoni).

(2) Combined with the above we often find obliterative shading (Thayer's principle), with, or without, a superimposed disruptive colour pattern (see Plates II and XIX).

(3) Attention has been drawn (Part I) to a special aspect of disruptive coloration, namely a type of pattern which is strengthened in its effectiveness by the extension of parts of the pattern-picture across separate, but adjacent parts of the animal's body. Very striking, and here comparable, are the cases of those patterns which extend continuously from fore to hind wings,—on the under surface of many butterflies* and on the upper surface of many moths† belonging to several families,—and across the segments of the hind legs in several families of Anura (including Hylidae, Bufonidae, Ceratophryidae, Pelobatidae, Ranidae, Rhacophoridae, Brevicipitidae, Brachycephalidae, and Phrynomeridae).

* as in Kallima sp., Grapta c-album, Thecla phaleros.

† as in Timandra amata, Pseudophia lunaris, Coremia unidentaria.

(4) Isolated distractive markings, such as eye-spots, which occur commonly near the posterior wing margins in Lepidoptera (*Thecla*, *Epinephele*, *Lycaena*, *Caligo*) and on the sacral region in Anura (*Mantipus ocellatus*, *Edalorhina perezi*, *Gastrophryne elegans*, *Eupemphix nattereri*).

(5) Flash colours, as in Cicadidae (*Hemisciera maculipennis*) Tettigoniidae (*Oedipoda miniata*), Lepidoptera (*Catocala electa*), and in several families of frogs (*Phyllomedusa hypochondrialis*, *Hyla versicolor*, *Arthroleptis stenodactylus*, *Hylambates maculatus*).

(6) Special protective resemblance to specific natural objects:-

(a) to *leaves*, - as in numerous butterflies and moths (*Kallima*, *Melanitis*, *Timandra*, *Phyllodes*), Phasmidae (*Phyllium*), Tettigoniidae (*Eurygnathus*, *Phylloptera*, *Tanusia*), and in the remarkable South American toad *Bufo typhonius* (Pl.XIV) whose habits and appearance have been described elsewhere (Cott,14); and in the Wood Frog (*Rana sylvatica*) (88) ;

(b) to *bark*, - as in butterflies (*Ageronia*) and moths (Sphingidae, Geometridae and others), beetles (Cerambycidae), and in tree frogs such as the large East African *Chiromantis xerampelina* (Pl. XVI,2):

(c) to *lichen*, - as in numerous procryptic moths (*Agriopis*, *Moma*, *Pachys*, *Bryophila*), beetles (*Lithinus*), and in the tree frog *Hyla langsdorfii* (Plate IV.),

(d) to twigs and stems (if we

extend the analogy to include reptiles) as in the tree snakes Oxybelis acuminatus in South America (Pl.XVI,1) and Thelotornis kirtlandii (Cott, 23) in East Africa, which take the place occupied by such Insecta as the stick insects (Phasmidae) and Geometrid larvae.

Associated with these procryptic colours and patterns, and also common to both Insecta and Anura, is the instinctive habit of "freezing" or remaining still in the presence of the enemy. This instinct, which is of such vital importance (for without it concealment is impossible) appears to reach its highest development in those species whose form and colouring are most specialised for concealment, as, for instance, among insects in the Geometrid larvae (which move and feed only by night and possess remarkable adaptations to render stillness possible during the hours of daylight), and among Anura in Bufo typhonius. I have referred elsewhere to the procryptic habits of this little toad, which "remained quite motionless while I arranged my tripod within a few inches, focussed the camera, and took several time exposures; nor did it make any attempt to escape when it was picked up, but allowed itself to be handled without a struggle, evidently relying on the "crouching habit" to escape observation - just as a young Stone Curlew will do under similar circumstances." (14)

2. The Theory of Warning Colours as applied to the Anura.

It is interesting to extend the application of the theory of warning colours from the Insecta to the Anura, and to determine to what extent the various features of aposematic colouring in the former group find their analogy here.

The generally accepted view that the warning colours of "defended" animals have been developed by the operation of natural selection rests upon the following classes of evidence:-

(1) The possession of some unpleasant attribute, such as poison, dangerous powers of attack, offensive secretions, repulsive odour or taste, or other features which render an animal dangerous or distasteful to potential predatory enemies.

(2) The presence of an advertising mechanism. This may take any of several forms, such as brilliant coloration (black, black and yellow, black and red, etc.), conspicuous colour pattern (spots, bands, stripes, etc.), or warning attitudes, movements or sounds.

(3) The fact that mammals, birds, snakes and other predatory vertebrates do not instinctively discriminate between palatable and unpalatable prey. They must first test everything experimentally in the light of individual experience.

(4) They have retentive memories, and when an animal is found by experience to possess dangerous qualities, it has only to be seen to be avoided.

(5) Warning colours are of vital benefit to their possessors, whose unpleasant qualities they advertise, by assisting the rapid education of enemies.

i. The Efficiency of Poisonous Secretions in defending Anura from Predatory Attack.

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. Typical "warning" features, namely, conspicuous colours (black, black and white, black and yellow, black and red) and bold patterns (stripes, bars, ocelli, etc.), combined with aposematic habits, are found in many species, and, where these occur, they appear to be characteristically associated with highly poisonous secretions.

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 (12):- "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 daytime 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 (37) : "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 (37).

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...." (27).

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 (130).

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" (37).

Referring to the East African toad Nectophrynoides vivipara, Loveridge (61) 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 (Pl. XXII). 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." (88)

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."

Noble says of the African Phrynomantis bifasciata, (Pl. XXI) that it also has "been found under certain circumstances temporarily to inflame the hands of the collector" (88) , and that both this and the previous species produce great quantities of milky secretion.

Loveridge (61) also refers to the skin secretion of P. bifasciata, which he says causes an irritation entirely comparable to that produced by stinging nettles.

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 (37): "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 beyond doubt the effectiveness of skin secretions in defending certain Anura from predatory attack. We must now discuss briefly the evidence of discrimination on the part of predatory enemies of the Anura.

ii. Power of Discrimination in Snakes and Birds.

The predatory enemies of frogs have been discussed in some detail elsewhere (20), and it has been shown that chief among these are birds and snakes. Of the former, few, if any, are exclusively frog-eaters. But many species include frogs in their diet, and in some cases these form the most important item of food (32, 55, 58, 59, 114, 129). Snakes are the most important enemies of the Anura, and not a few species live on frogs to the exclusion of almost all other food (4, 27, 33, 58, 87, 199) These animals depend largely upon vision in hunting for prey (27, 66).

A vivid account by Ditmars, which I have quoted in full elsewhere (Cott, 25 , p. 112) well illustrates the important place occupied by vision in the hunting of prey in the case of the snake Eutenia saurita. There is a considerable body of evidence that both birds and snakes learn to discriminate between poisonous frogs and those which are relatively palatable (10, 25, 27, 37, 73, 94) We may mention in passing the following observations, which besides providing additional evidence of the effectiveness of skin-secretions in defending Anura against predatory attack, are especially significant in relation to discrimination by predators.

Ditmars (27) has proved beyond question that the King Cobra (Naia bungarus) is able to distinguish immediately between the harmless Water Snake (Tropidonotus taxispilotus) and the poisonous Water Moccasin (Ancistrodon piscivorus). The same authority states that "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." 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 (33). Budgett (10) 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." 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 unpalability 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..."

It appears, then, from the above considerations, that there is a close parallelism in the application of warning colours to Insecta and Anura respectively. In each case, the same conspicuous combinations of colours (black, black and red, etc.) and striking patterns (bars, ocelli, stripes, etc.) are found associated with nauseous or dangerous qualities which

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

render their possessor relatively inedible: in each case respective vertebrate enemies are known to form associations and to learn by experience to avoid dangerous or unpalatable prey on sight. In leading to immediate recognition (and by thus accelerating the education of enemies) the conspicuous attribute is believed to be of vital benefit to its possessor.

PART III. OBSERVATIONS ON THE FEEDING-HABITS AND ECONOMIC STATUS OF TREE FROGS IN THE LOWER ZAMBESI VALLEY, AND IN GRAN CANARIA.

In investigating the food-habits of an animal, and the light which they throw upon the relation between colour and edibility in insect-prey, as revealed by the examination of stomach contents, it is necessary to obtain quantitative data. There is still considerable disagreement among biologists as regards both the origin and significance of warning and procryptic coloration, and at present what we want are not new theories, but new facts. Especially is this the case regarding the feeding-habits of batrachians, which have rarely been studied in relation to these problems. Isolated or casual records (such as "food chiefly insects," "two stomachs contained mostly spiders," etc.), which sometimes figure in systematic publications, are of but little value either as an indication of a frog's diet in general, or in particular as evidence of the part which adaptive coloration plays in protecting insects from their enemies, and such observations are apt to be misleading.

The present Part contains an account of the food-habits of certain tree-frogs, and a tabulation of the food animals derived from the stomachs of 993 individuals belonging to eight species.

Representing some 12,638 insects and other prey, this material is the outcome of a detailed investigation of food eaten under natural conditions. It is believed to be sufficiently plentiful to furnish reliable data (1) for testing the efficiency of procryptic and warning colours, and mimicry, in defending certain insects from predatory attack, and (2) as an indication of the part played by these batrachians in the production of adaptive coloration in insects.

1. The Food of certain Species in Portuguese East Africa.

11,428 insects and other food-animals were obtained from the examination of 798 tree-frogs belonging to the following species:- Hyperolius marmoratus, H. bayoni, H. argus, Megalixalus fornasinii, M. brachycnemis, Leptopelis johnstoni, and Phrynobatrachus acridoides.

The figures in Table II show (1) the number of frogs examined of each species respectively, (2) the number, and (3) percentage which contained recognizable food, (4) the total number of food-animals per individual, and (5) the average number of food-animals per individual.

TABLE ~~III~~ II

Species.	Number examined.	Number containing food.	Per-centage.	Total food-content.	Mean food-content.
H. mormoratus	40	38	95	2675	66·9
H. bayoni	110	107	97	3688	33·5
H. argus, ♂♂	132	?	?	2074	15·7
H. argus, ♀♀	122	?	?	1226	10·0
M. fornasinii	360	245	68	1119	3·1
M. brachycnemis	11	9	82	31	2·8
L. johnstoni	8	6	75	13	1·6
P. acridoides	15	15	100	602	40·1

An analysis of the food-animals is summarized for each species in Table III.

The foregoing material is classified in percentages according to the food-preferences of each species respectively, as follows:-

H. marmoratus (40).... (Prey 2675).	Ants, 97.53; beetles, 1.05; Diptera, .44; bugs, .34; spiders, .30; Orthoptera, .15; Hymenoptera (other than ants), .11 Lepidoptera, .08.
H. bayoni (110)....... (Prey 3688).	Ants, 96.18; bugs, 1.57; beetles, 1.27, Diptera, .43; Lepidoptera, .16; spiders .13; Orthoptera, .11; termites, .06; dragonfiles, .03; woodlice, .03; Hymenoptera (other than ants), .03.
H. argus ♂♂ (132)..... (Prey 2074).	Ants, 94.68; bugs, 2.60; beetles, 1.31; Diptera, .58; spiders, .34; Orthoptera .19; Lepidoptera, .15; dragonflies, .05; woodlice,.05; hymenoptera (other than ants- .05.
H. argus ♀♀ (122)..... (Prey 1226).	Ants, 91.17; bugs 2.54; beetles, 1.80; Diptera, 1.56; Orthoptera, 1.22; Lepidoptera, .98; Arachnida, .57; Hymenoptera (other than ants), .16.
M. fornasinii (360)... (Prey 1119)	Bugs, 46.3; Diptera, 26.3; ants, 10.8; beetles 7.1; Lepidoptera, 4.8; spiders, .9; Orthoptera, 1.9; dragonflies, .9; Hymenoptera (other than ants), .8; woodlice, .2.
M. brachycnemis (11).. (Prey 31.)	Ants, 77.3; bugs, 9.7; beetles, 6.5; Diptera, 6.5.
L. johnstoni (8)...... (Prey 13)	Ants, 23.1; Caterpillars, 23.1; beetles 23.1; crickets, 15.3; bugs, 7.7; Batrachia, 7.7.
P. acridoides (15).... (Prey 602).	Ants, 91.87; Diptera, 5.65; beetles, 1.16; Hymenoptera (other than ants), .49; bugs, .33; spiders, .33; Orthoptera, .17.

It will be seen that there is a close general resemblance in the habits of H. marmoratus, H. bayoni, and H. argus. In each case ants form a high percentage of the food eaten

TABLE IV.—Classification of Food-Animals (complete or fragmentary) recovered from the alimentary track of 798 Tree-Frogs.

		Hyperolius marmoratus.	*Hyperolius bayoni.*	*Hyperolius argus,* ♂♂.	*Hyperolius argus,* ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Total.
		40	110	132	122	360	11	8	15	798
CRUSTACEA.	Isopoda	...	1	1	...	2	...	...	...	4
ODONATA.	Agrioninæ ?	...	1	1	...	10	...	...	...	12
ORTHOPTERA.	Forficulidæ	2	1	3	5	5	...	...	...	16
	Blattidæ	1	1	...	4	9	...	...	...	15
	Gryllidæ	1	1	1	3	1	...	2	1	10
	Acridiidæ	...	1	...	3	7	...	...	...	11
ISOPTERA.	Termitidæ	...	2	...	...	...	...	...	...	2
HEMIPTERA.	Heteroptera (large)	...	3	1	4	6	...	...	...	14
	Various Hemiptera (small).	...	10	9	2	12	...	...	2	35
	Peregrinus maidis	8	41	44	25	77	2	1	...	198
	Aphididæ	1	4	...	1	423	1	...	...	430
COLEOPTERA.	Rutelidæ	...	1	...	5	1	...	...	...	7
	Various large	...	2	...	4	4	...	2	...	12
	Various medium	13	...	3	1	8	...	...	...	25
	Various small	15	44	24	12	66	2	1	7	171
DIPTERA.	Muscidæ, etc.	6	12	6	9	162	2	...	...	197
	Culicidæ, etc.	6	4	5	10	132	...	...	2	159
	Larvæ	...	...	1	...	...	...	...	32	33
LEPIDOPTERA.	Adult insects	1	5	1	4	26	...	...	...	37
	Larvæ	1	1	2	8	28	...	3	...	43
HYMENOPTERA.	*Pheidole megacephala* (worker).	2599	3533	1962	1111	119	24	3	543	9894
	,, ,, (soldier).	8	14	2	4	1	...	...	9	38
	Monomorium subopacum	2	...	...	1	1	...	...	...	4
	Camponotus sp.	...	...	...	...	...	...	...	1	1
	Various large	2	1	1	3	3	...	...	...	10
	Various small	1	...	...	...	6	...	...	3	10
ARACHNIDA.	Acarina	...	...	...	1	...	...	...	...	1
	Araneida	8	5	7	6	10	...	...	2	38
BATRACHIA.	*Hyperolius* sp.	...	...	...	...	...	...	1	...	1
Total		2675	3688	2074	1226	1119	31	13	602	11428

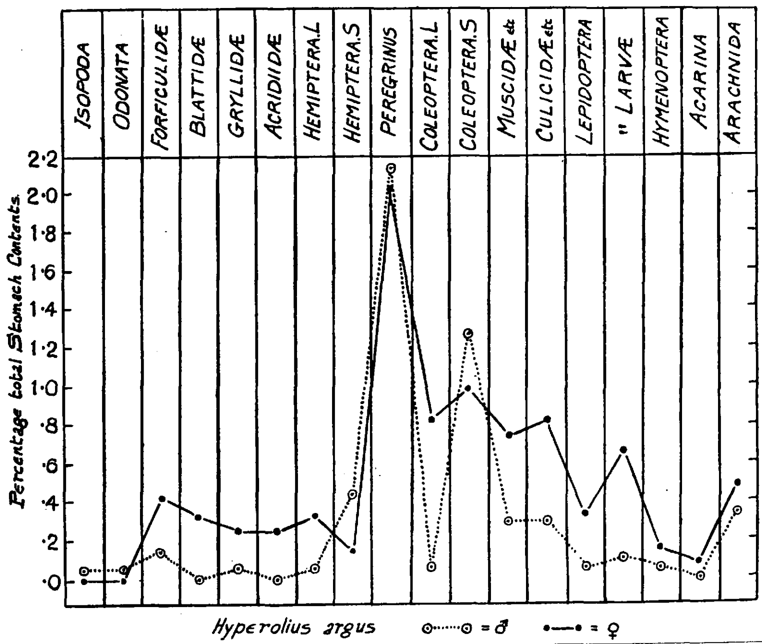
(over 90 per cent.) - beetles, bugs, and flies, in varying proportions, taking the three succeeding places in order of preference.

In the case of H. argus it has been shown by Parker (90) that the present series from the Lower Zambesi exhibits remarkable sexual dichromatism. If the difference in the colour of the sexes (Plate I) has raised some complications regarding the synonymy of the species (as discussed by Parker), it certainly also raises points of considerable interest in ecology. For not only are the sexes markedly differentiated in colour, and to a less extent in size, but also, apparantly, they differ both in their feeding habits, and their habitat. The general habits of the frogs have been mentioned elsewhere (20) and we shall only refer here to the question of food.

If we exclude ants from the picture, and examine the remaining food eaten by males and females respectively of H. argus, certain fairly well-marked differences in the matter of food-habits will be noticed. These are well brought out in text fig. 2 .

Examination of this graph shows that, broadly speaking, the males favour smaller insects, while the

Text-figure 2.

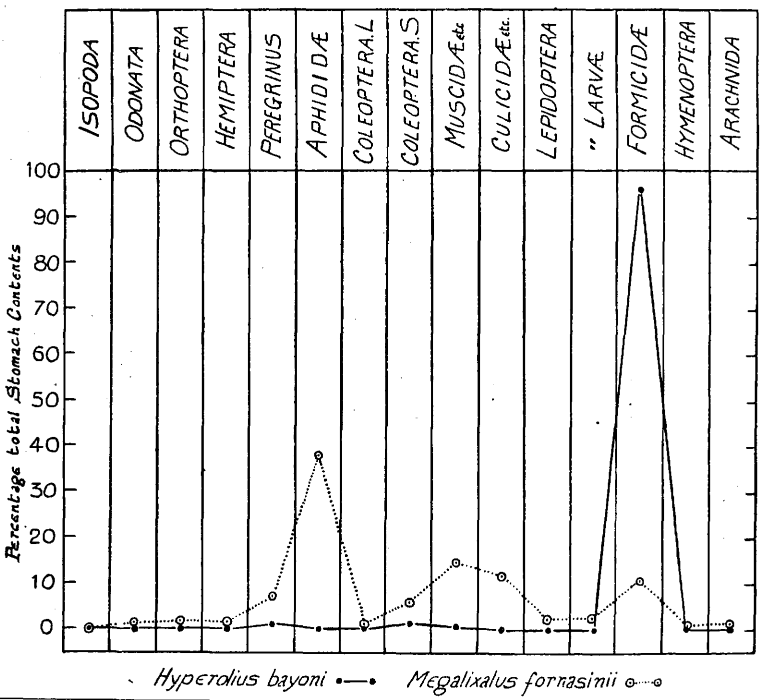


Food-preferences of H.argus, ♂♂ and ♀♀, as shown by percentage analysis of stomach contents. Ants are omitted from the diagram. "L" and "S" indicate relatively large and small insects respectively.

females are able to tackle heavier quarry - in fact, the differences in feeding habits appear to be correlated with the differences in the size of the sexes. Thus the females eat a higher percentage of earwigs, cockroaches, crickets, grasshoppers, large beetles, large bugs, Diptera, and Lepidoptera; males, on the other hand, make up on smaller bugs and beetles and on a higher percentage of ants.

In contrast to the species of <u>Hyperolius</u>, <u>M. fornasinii</u> is essentially a fly-catcher, large muscid Diptera making the bulk of its food. These differences,

Text-figure 3.



Food-preferences of <u>H.bayoni</u> and <u>M.fornasinii</u> as shown by percentage analysis of stomach contents.

which are discussed in parts I and IV, are clearly shown in text-fig. 3 , where the graph referring to <u>H.bayoni</u> may be regarded as typical also of <u>H.marmoratus</u> and <u>H.argus</u>.

2. The Food of Hyla arborea var, meridionalis in Gran Canaria.

The analysis of this material will be found in Table IV ., which is arranged to show (1) the number of food-animals eaten, and (2) the number of frogs from which various groups of prey were recovered.

Table IV. - Analysis of Food-animals (complete or fragmentary) recovered from the Alimentary Tract of 195 Tree-frogs from Gran Canaria and Gomera, showing (i) the Systematic Distribution of Prey, and (ii) the number of Individual Tree-frogs containing different Groups of Food-Animals.

Prey.	(i.) Food-animals eaten.		(ii.) Frogs containing food.	
	Number.	Per cent.	Number.	Per cent.
Isopoda	47	3·88	23	12·5
Amphipoda	2	·17	2	1·1
Orthoptera	13	1·07	11	6·0
Hemiptera	43	3·55	36	19·6
Coleoptera	200	16·54	104	56·6
Diptera	74	6·12	33	17·9
Neuroptera	2	·17	2	1·1
Lepidoptera	37	3·06	27	14·7
Hymenoptera: Ants	695 } 704	57·44 } 58·18	136 } 137	74·0 } 74·6
,, Other than ants	9	·74	7	3·8
Araneæ	70	5·78	54	29·3
Acarina	9	·74	8	4·3
Chilopoda	9	·74	6	3·3

Certain other data, given for comparison with figures and Table III in my earlier paper (20, p. 485), are as follows:-

Number of frogs examined..............................195
Number containing recognizable food..................184
Percentage containing recognizable food............. 94
Number of food-animals obtained.....................1210
Average number of food-animals per individual...... 6.2

Classified in percentages, according to preference the food is as follows:-

ants, 57.44; beetles, 16.54; Diptera, 6.12; spiders, 5.78; woodlice, 3.88; bugs, 3.55; Lepidoptera, 3.06; Orthoptera, 1.07; Hymenoptera (other than ants), 0.74; mites, 0.74; centipedes, 0.74; Neuroptera, 0.17; Amphipoda, 0.17.

It has been shown elsewhere (20,pp.525-527) that frogs toads, and tree-frogs are typically enormous feeders. Although in the present species the mean food content is low, some individuals had stomachs stuffed almost to the bursting point. The single example may be cited of a female from Fataga measuring 44 mm. in length. The hugely distended stomach of this frog contained four large freshly caught weevils (_Hyperstichus eremita_), in almost perfect condition, each measuring about 14 mm., and the remains of a fifth large OEdemerid beetle (_Ditylus concolor_), also measuring 14 mm. In addition there was a quantity of débris in the intestine and rectum.

3. Tree-Frogs in the Economy of Nature.

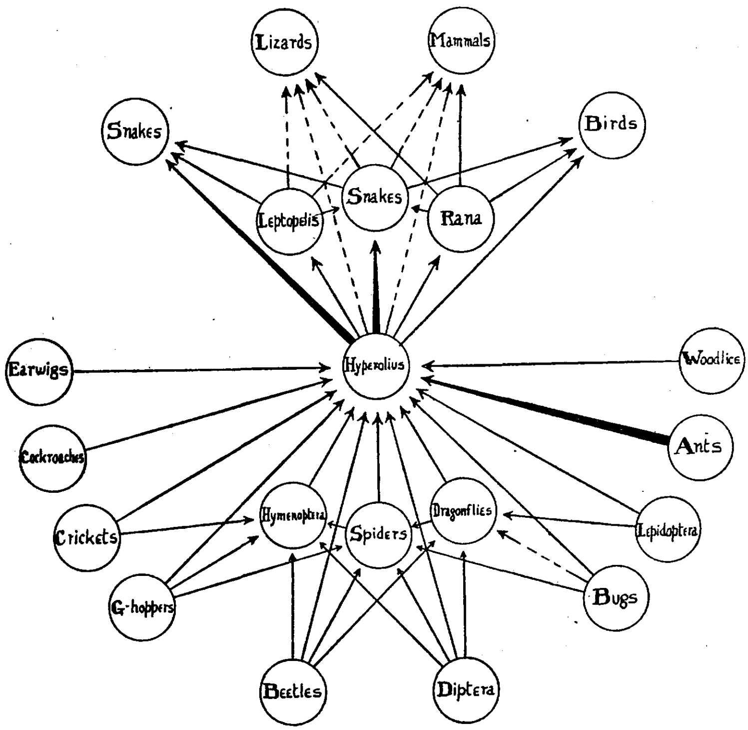
Having considered in some detail the enemies and prey of tree-frogs such as _Hyperolius_ and _Megalixalus_, we can now look back in an attempt to see how these frogs stand in relation to the economy of tropical nature.

The efficiency of certain adaptations in insects (p. 46) and in frogs (pp. 5 , 14) is dealt with elsewhere. It is with one aspect of the struggle for existence - the competition for food and safety, and the network of interrelations between predator and prey, that we are here concerned.

At the present time we know little about the regulation of animal numbers in the tropics. It is only possible to take up here and there a thread of that vast fabric woven of biological interrelationships, which, with its every changing pattern, appears more complex and remarkable the closer it is studied.

In order to illustrate this point, it will be convenient to consider in particular the case of the genus Hyperolius, respecting which we have the most complete data. In text-fig. 4 an attempt has been made to show diagrammatically the position of these frogs in relation to other animals with which they are associated in nature, and with which, in the capacity of predator or prey they come into vital contact. The tree-frogs are shown in the centre of the diagram, surrounded (beneath) by their food-animals and (above) by their enemies. The arrows

Text-figure 4.



Simplified diagram indicating the position in nature of *Hyperolius*, considered in relation to its enemies and its prey.

in all cases point from prey to predator, indicating the direction of food-transference - proceeding (generally) from the smaller, more numerous, and more defenceless to the larger, bolder, or more resourceful animal. I have indicated (1) with heavy arrows what appear to be the most important relationships; (2) with continuous lines those established by my own observations, supplemented by the records of other naturalists; and (3) with dotted lines some cases which are doubtful. No claim is made that this simplified diagram of food-relationships is complete. It does, however, serve to indicate clearly some of the intricate 'food-chains' in which the frogs form an essential link. These chains, considered together, are more closely analagous to a network, where each strand crosses and reacts upon others, in maintaining the complex and constantly varying balance of life.

We are still, unfortunately, very ignorant about the enemies of Hyperolius, and have little data to work upon. But there is little doubt that snakes are the enemy mainly responsible for keeping their numbers in check. (Cott 20 pp.482-484).

When we come to consider the food-animals, we can speak with more certainty. The frogs indulge in a wide range of diet, comprising at least eleven arthropod orders. Their activities involve the destruction of animals which are both useful and harmful to man. Among the former we must reckon insect-destroyers such as parasitic and predatory Hymenoptera, dragonflies, and spiders; among the latter, grasshoppers, aphids, and other injurious bugs, beetles, caterpillers, flies, gnats, and mosquitoes.

It is beyond the scope of this paper to discuss the economic importance of tree-frogs as destroyers of insect life. In regions like the lower Zambesi valley, where the frogs are abundant, the numbers of insects killed must be enormous. An idea of the extent of their depredations may be obtained by referring to the right-hand column of Table II where I have given the average number of food-animals obtained from an individual of each species examined. These figures, being calculated from the stomach-contents of individuals in all states of hunger and repletion, including those with empty stomachs, we may regard a tolerably full meal as comprising twice the amount.

To illustrate this point we may cite two examples, which indicate how insect numbers may be effected by their depredations The average stomach-content of an individual H. marmoratus is 67 insects. Assuming that the frog eats a full meal of 134 insects in twenty-four hours, the creature will destroy nearly 49,000 insects during the year. Or again, taking all species of Hyperolius collectively, the average number of ants recovered from all (including empty) stomachs in the present series is 23. This figure is obtained from the examination of 404 individuals. Now we may regard a full meal as comprising twice this amount, or about 50 ants (besides other insects), a figure which was often very far exceeded (See 20, p.516)

If we assume that an acre of, say, banana or maize plantation supports 500 Hyperolius individuals, these frogs will, in the course of the year, devour no fewer than 9,125,000 ants - probably an underestimate, if we allow, on the observations of Kirkland (See 20,p.526) that the stomach is filled not once, but six times, in twenty-four hours.

An examination of individual stomach-contents reveals the same story. Lack of space prevents the recording of more than a few examples, which illustrate sufficiently well the effect which the frogs' depredations may be calculated to have in the regulation of insect numbers. (See 20,pp.516,526-27).

H. marmoratus: (1) 1 muscid fly, 232 ants; (2) 1 cockroach, 2 beetles, 1 muscid fly, 93 ants; (3) 3 Culicidae?, 44 ants, 1 braconid. H. bayoni: (1) 1 homopterous bug, 106 ants; (2) homopterous bugs, 1 beetle, 81 ants; (3) 1 homopterous bug, 2 beetles, 1 culicid, 2 Lepidoptera, 52 ants. H. argus: (1) 9 homopterous bugs, 1 beetle, 24 ants; (2) homopterous bugs, 1 beetle, 3 culicids, 19 ants; (3) 1 earwig, 1 cricket, 2 homopterous bugs, 1 spider. M. fornasinii: (1) 3 homopterous bugs, 1 beetle, 2 muscid Diptera, 7 Culicid, etc., 2 hymenopterous insects, 1 spider; (2) 146 aphids, 2 beetles, 1 ant; (3) 7 muscid Diptera, 1 culicid; (4) 47 aphids, 4 beetles, 10 culicid, etc., 3 ants. P. acridoides: (1) 24 dipterous larvae, 59 ants; (2) 1 gryllid, 3 beetles, 27 ants, 1 proctotrypid.

Bearing in mind the abundance of tree-frogs in suitable localities - and in the light of the above observations, - I believe these small batrachians must be reckoned a not insignificant factor in the regulation of insect numbers in the tropics; and I suggest it is probably that the frogs, which appear to touch human affairs so lightly, render a not inconsiderable service to man by reducing the hosts of pestilential or injurious insects which so notoriously rob him of his crops, his health, and his peace of mind.

A comparison of the biological status of *Hyla arborea* var. *meridionalis* in Gran Canaria with that of the tree frogs considered above throws some light upon an important aspect of animal life, namely, upon the fundamental, and often detailed, similarity in the organization of different animal communities. This question, and the conception of the ecological "niche," have been discussed in general terms elsewhere (Cott, 22, p.315). The principle is beautifully illustrated by reference to certain of the present species.

Almost wherever frogs occur some species are to be found which have left the sod for an arboreal existence. This widespread habit of climbing has arisen independently in several families. There is, in fact, an almost world-wide tree-frog niche. This niche is filled by certain Brachycephalidae - *Dendrobates* in South America; by a Bufonid genus *Nectophryne* in India and Borneo; by the Ceratophryid genus *Hylodes* in South America; by the majority of Hylidae, such as

Hyla, an almost cosmopolitan genus, and *Nototrema* and *Phyllomedusa* in South America; by several Ranid genera, such as *Cornufer* in Papua and Fiji, and *Staurois* in Malaya and Borneo; by Amphignathodontidae - *Amphignathodon*, in South America; by many Rhacophoridae, such as *Chiromantis*, *Leptopelis*, *Hyperolius*, and *Megalixalus* in Africa, *Mantidactylus* and *Mantella* in Madagascar, and *Rhacophorus* in Madagascar, Southern Asia, Japan, and the Philippines; and, finally, by the Brevicipitid genus *Platyhyla* in Madagascar.

Here, then, we have frogs belonging to different families, inhabiting widely separated regions, representing parallel but independent adaptations to an arboreal existence, and occupying a particular relationship to the community.

What this relationship is may be discovered, at any rate in part, by investigating their food-habits.

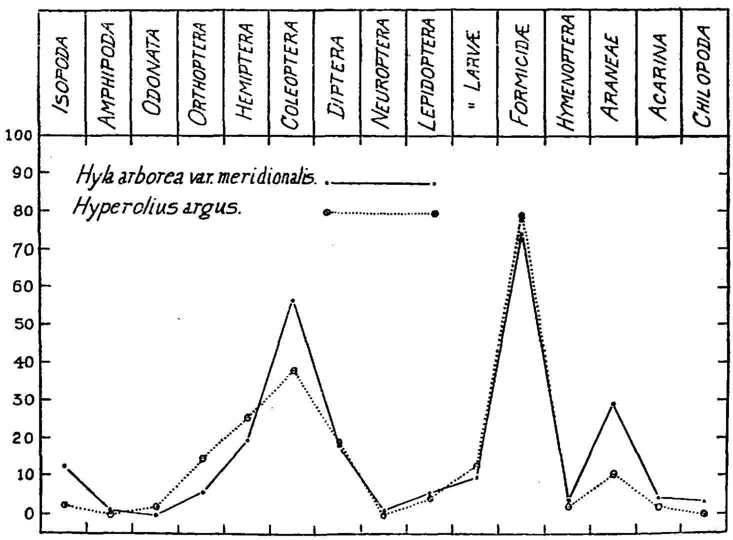
When this is done a remarkably close parallelism is found to exist between certain species, as in the case of *Hyla arborea* in Gran Canaria and *Hyperolius argus* in Portuguese East Africa. These two frogs - unrelated and inhabiting widely separated regions - closely resemble one another in form, in the habitat in which they elect to seek food and shelter, and in the food that is actually eaten. In other words both, in their respective communities, have precisely the same status; both, in their respective environments, occupy precisely the same station. The parallelism is clearly brought out by a comparison of food preferences, as indicated by the number of individuals containing various groups of prey. The figures, in order of preference, are as follows:-

Hyperolius argus .. (47 specimens).	Ants, 37; beetles, 18; bugs, 12; Diptera, 9; Orthoptera, 7; caterpillars, 6; spiders, 5; Lepidoptera (adults), 2; woodlouse, 1; dragonfly, 1; Hymenoptera (other than ants), 1; mite, 1.
Hyla arborea ...... (184 specimens).	Ants, 136; beetles, 104; spiders, 54; bugs, 36; Diptera, 33; woodlice, 23; caterpillars, 18; Orthoptera, 11; Lepidoptera (adults), 10; mites, 8; Hymenoptera (other than ants), 7; centipedes, 6; Neutoptera, 2; Amphipoda, 2.

This parallelism in food-preference is shown graphically in text-fig. 5.

Further, a comparison of the prey itself of East African tree-frogs and of the present species also brings out a general resemblance between the orders and families

Text-figure 5.



eaten, this correspondence extending to some genera and species, as shown in the following list of prey common to the frogs in both regions:-

Hyla arborea.	*Hyperolius argus.*
Hemiptera.	
Lygaeidae.	
Dieuches armipes (F.)	*Dieuches umbrifer* Stål. *Dieuches spp.* (2).
Coleoptera.	
Coccinellidae.	
Scymnus canariensis Woll. *Scymnus cercyonides* Woll.	*Scymnus trepidulus* Weise.
Curculionidae.	
Calandra oryzae L. *Apion rotundipennis* Woll. *Apion sagittiferum* Woll. *Apion umbrinum* Woll. *Apion* sp.	*Calandra oryzae* L. *Apion* sp.
Diptera.	
Tipulidae.	
Gonomyia tenella Mg.	*Gonomyia* sp.
Muscidae.	
Musca domestica L. *Musca tempestiva* Fall. *Limnophora* sp.	*Musca autumnalis* de Geer ? *Musca* sp. *Limnophora* sp.
Hymenoptera.	
Formicidae.	
Pheidole (Pheidole) Megacephala F. *Monomorium subopacum* Smith.	*Pheidole megacephala* var. *punctulata* Mayr. *Monomorium supopacum* var. *australe* Emery.

Camponotus (Camponotus) vagus Scop. Camponotus (Myrmentoma) libanicus Andre.	Camponotus sp.

From what has been said above it will be seen that a niche, in certain cases at any rate, represents a very definite status in the animal community; that this status depends essentially upon food-relationships; that the study of niches is a step towards understanding the community as a whole; and that this study points to a fundamental similarity of organization in different animal communities.

PART IV. THE FEEDING HABITS OF THE ANURA, WITH SPECIAL REFERENCE TO THE THEORY OF WARNING COLOURS.

1. Methods of Investigation, and Material.

The theories of warning colours, mimicry, and protective resemblance depend essentially upon two classes of evidence - namely, that a certain relationship exists between coloration and palatability in insects and other animals, and that different insectivorous enemies discriminate in the choice of food.

Palatability or distastefulness of the prey and differential preferences of the predator lie at the root of the matter.

The efficiency of protective adaptations of insects in relation to predatory enemies may be investigated in a variety of ways, namely: by direct observations in the field on the feeding-habits of insectivorous animals; by properly conducted feeding-experiments with animals either in captivity or under natural conditions; by a study of the ecology and adptations of the insects themselves; or by the examination of the stomach- and pellet-contents of wild animals. (1) Of these, the first method is of prime importance. Unfortunately, the difficulties attending accurate observation and exact identification under these circumstances are great, and information from this source is as hard to obtain as it is valuable. (2) The experimental method, which has generally been adopted in preference to any other as a source of evidence regarding the relative palatability of insects, has much to recommend it. It is, however, sometimes open to the criticism that the conditions of captivity distort the food-relations of animals, modifying the results of the experiments so as to render them untrustworthy. This view is put forward in a very vigorous criticism by McAtee (67). The careful and detailed experiments of Marshall, Poulton, Carpenter, Swynnerton, and others in themselves supply an answer to most of the difficulties suggested by this writer, whose objections are dealt with in detail by Swynnerton (112), pp. 203-226). No one would deny that the experimental method of investigating the food preferences of insectivorous animals is one beset with difficulties, but these are certainly not insuperable, as McAtee apparently supposes, and this method has yielded a vast amount of invaluable data bearing upon the theories of mimicry and of procryptic and warning coloration. (3) Much indirect evidence is afforded by field observations on the habits of insects, notably the resting position, method of flight, and general habits considered in relation to habitat, as well as by "the comparative study of colour-patterns and structure" (65), including defensive features such as stings, offensive secretions, tough exoskeleton, etc. (4) Many authorities are agreed that our knowledge of the subject must come in the main from the evidence of stomach- and pellet-examination. This method, when carried out on a large enough scale, furnishes data of value and accuracy. In the stomach-contents of wild animals we have documentary evidence - beyond the reach of critics - of the actual food eaten by a species under natural conditions. This is, and must be, the final court of appeal.

This investigation is based upon the food derived from the stomachs of 798 tree frogs, belonging to seven species, collected by the writer in Portuguese East Africa, and of 195 tree frogs (*Hyla arborea* var. *meridionalis*) from Gran Canaria.

2. The Efficiency of Warning Colours, Mimicry, and other Protective Adaptations in Insects as a Defence against Tree Frogs.

The present section deals with the usefulness of various adaptations (especially procryptic and warning coloration, and mimicry) in protecting insects against the predatory attacks of batrachian enemies. In other words, we have to consider what light the feeding-habits of these animals throw upon the relation which is supposed to exist between colour and edibility in insects.

The subject is most conveniently studied in reference to the various insect groups severally. These are considered below in detail.

The food-animals have been classified into groups based upon the colour classification adopted by Prof. Hale Carpenter in his 'Experiments on the Relative Edibility of Insects' (12):-

AA. Typically aposematic insects exhibiting warning colours (black, black and yellow, black and red, etc.) and conspicuous patterns (spots, bands, stripes, etc.).

A. Aposematic, but less conspicuous than the above.

C. Insects whose colour scheme is of doubtful significance and which do not readily fit into any of the other groups.

P. Dull or obscurely marked insects.

PP. Typically procryptic insects, showing a marked degree of protective resemblance.

In assessing the status of an insect in reference to conspicuousness or concealment, account must be taken not only of form, coloration, and pattern, but also of the creature's size, habits, and habitat:

(1) Of size, because a large advertisement is more efficient than a small one; and conversely because a small object is more easily concealed than a large one.

(2) Of habits, because conspicuousness may be increased by habitual behaviour, such as gregarious habits and displays of colour; while other factors, such as

procryptic attitudes, hiding, immobility, dropping, death-feigning, and nocturnal habits make for concealment.

(3) Of habitat, because conspicuousness and concealment depend essentially upon the degree of contrast between an object and its surroundings. A red coccinellid beetle resting on a red-brick building may appear as procryptic as a green weevil on a nettle-leaf. Yet the former, seen in its natural surroundings, is a highly conspicuous insect.

From these considerations it is obvious that a classification of insects according to visibility by an enemy depends upon a number of factors. Such a classification must be to an extent arbitrary; and there must occur doubtful or borderland cases not certainly referable either to aposematic or procryptic groups.

The figures in Tables V-X, XV-XVII refer to such food-animals as were sufficiently well preserved for critical examination.

i. Tree frogs from Portuguese East Africa.

Isopoda.

Woodlice, although abundant and easily accessible, are hard unsatisfactory things to eat, and they appear to be little preyed upon by the tree-frogs investigated. Only four specimens were obtained, two from M. fornasinii, and one from H. bayoni and H. argus, respectively.

TABLE V.

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Totals.	Remarks.	Colour-group.
	ORTHOPTERA.											
	FORFICULIDÆ.											
1	*Diaperasticus erythrocephalus* Ol.	...	...	1	1	1	...	...	...	3	Large; dark brown, tegmina with straw-coloured stripes.	P
2	Gen. indet.	2	1	2	3	4	...	...	1	13	Medium-sized; inconspicuously coloured.	P
	BLATTIDÆ.											
3	*Blattella germanica* Linn.	...	...	...	2	...	...	...	...	2	Large; light brown, with dark brown marks.	P
4	*Blattella* sp.	...	...	...	1	3	...	...	...	4	Large; light brown, with darker marks.	P
5	Gen. indet.	1	1	...	1	6	...	...	...	9	Immature specimens; medium-sized; light brown.	P
	ACRIDIIDÆ.											
6	*Eumastacinæ* sp.	...	...	...	...	1	...	...	...	1	Medium-sized; inconspicuous colouring.	PP
7	*Trilophidia* sp.	...	...	...	...	2	...	...	...	2	Large; brown, with darker brown marks on wings; legs banded with brown.	PP
8	Gen. indet.	...	1	...	3	4	...	...	...	8	Medium-sized; inconspicuous.	PP
	GRYLLIDÆ.											
9	*Euscyrtus* sp.	...	...	...	...	1	...	...	...	1	Medium-sized; straw-coloured, with dull brown longitudinal marks.	PP
10	Gen. indet.	1	1	1	3	...	...	2	...	8	Large; pale brown, with greyish marks.	PP
11	*Gryllotalpa* sp.	...	...	...	...	...	...	...	1	1	Small; earth-brown.	PP

TABLE VI.

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Totals.	Remarks.	Colour-group.
	HEMIPTERA.											
	HETEROPTERA.											
	PENTATOMIDÆ.											
12	First-stage larva	...	...	...	...	3	...	...	...	3	Minute; reddish-brown and pink; first-stage nymphs.	AA
	COREIDÆ.											
13	*Cletus* sp.	...	...	...	...	1	...	...	...	1	Large; dusky brown.	P
	LYGÆIDÆ.											
14	*Nysius ståli* Evans	...	...	1	...	5	...	...	...	6	Medium-sized; buff, more or less heavily marked with dark brownish-grey.	P
15	*Dieuches umbrifer* Stål.	...	...	...	2	...	...	...	...	2	Large; head and thorax black, abdomen dark brown.	A
16	*Dieuches* sp.	...	...	...	...	1	...	...	...	1	Large; chestnut-brown.	A
17	*Dieuches* sp.	...	...	1	2	1	...	...	...	4	Large; brown, with lighter marks.	P
	PIESMIDÆ.											
18	*Piesma diluta* Stål	...	2	...	...	...	...	...	...	2	Very small; almost colourless.	PP
19	*Piesma* sp.	...	1	...	1	1	...	...	...	3	Very small; almost colourless.	PP
	GERRIDÆ.											
20	*Gerris* sp.	...	...	...	...	...	...	...	2	2	Very small nymph; light buff and brown.	P
	NABIDÆ.											
21	*Nabis capsiformis* Germ.	...	...	...	...	1	...	...	...	1	Elongated, slender form; procryptic; straw-coloured, with light brown mottling.	PP
	CAPSIDÆ.											
22	*Creontiades mimicum* Dist.	...	3	...	...	...	...	...	...	3	Large; light straw-coloured.	PP
23	*Lygus* sp.	...	...	...	1	...	...	...	...	1	Medium-sized; light buff, with obscure darker markings.	P
	HOMOPTERA.											
	JASSIDÆ.											
24	*Nehela* sp.	...	1	...	...	1	...	...	...	2	Small; procryptic; light buff, faintly streaked with green or brown.	PP
	DELPHACIDÆ.											
25	*Peregrinus maidis* Ashm.	8	41	44	25	77	2	1	...	198	Macropterous and brachypterous, ♂♂ & ♀♀; pale buff, banded with light brown.	P
26	*Dicranotropis*, sp. n.	...	...	...	...	2	...	...	...	2	Small; inconspicuous.	P
27	*Eurysa*, sp. n.	...	...	...	...	1	...	...	...	1	Small; brown, speckled with darker brown.	PP
28	*Delphacodes* sp.	...	...	...	...	2	...	...	...	2	Small; brown and pale buff.	P
29	Larvæ indet.	...	...	3	...	...	...	...	...	3	Small; inconspicuous colouring.	P
	DERBIDÆ.											
30	Larva indet.	...	...	1	...	...	...	...	...	1	Minute; buff.	P
31	*Kamendaka*, sp. n.	...	1	...	...	...	...	...	...	1	Small; colourless.	PP
	PSYLLIDÆ.											
32	Gen. indet.	...	1	...	...	...	...	...	...	1	Small; inconspicuous buff colouring.	P
	APHIDIDÆ.											
33	*Aphis maidis* Fitch.	...	...	...	...	423	...	...	...	423	Nymphs and adult insects; minute; light buff, brown or greyish.	P
34	*Aphis* sp.	1	4	...	...	...	1	...	...	6	Nymphs; brown or brownish grey.	P

TABLE VII.

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides*	Totals.	Remarks.	Colour-group.
	COLEOPTERA.											
	STAPHYLINOIDEA.											
	STAPHYLINIDÆ.											
35	*Conosoma* sp.	...	...	...	1	...	...	...	...	1	Small; brown.	P
36	*Oxytelus* sp.	...	...	1	...	...	...	...	...	1	Small; dull brown or blackish-brown.	P
37	*Pinophilus* sp.	...	...	...	...	1	...	...	...	1	Elongated, medium-sized; black, "unpleasant looking."	A
	PSELAPHIDÆ.											
38	*Reichenbachia punctulata* F.	...	...	...	...	1	...	...	...	1	Minute; brown.	P
39	Gen. indet.	...	...	...	...	1	...	...	...	1	Minute; inconspicuous brownish colouring.	P
	CORYLOPHIDÆ.											
40	*Arthrolips* sp.	...	...	...	...	1	...	...	...	1	Minute; polished dark brown.	P
	DIVERSICORNIA.											
	NITIDULIDÆ.											
41	*Haptoncus luteolus* Er.	3	...	1	1	5	...	...	...	10	Very small; dull drown.	P
42	*Carpophilus dimidiatus* F.	...	...	...	1	...	...	...	...	1	Very small; dull brown.	P
	LANGURIIDÆ.											
43	*Anadastus* sp.	...	...	...	..	1	...	...	...	1	Medium-sized; elongated, with metallic colouring.	A
	LATHRIDIIDÆ.											
44	*Corticaria* sp.	1	1	4	...	2	...	...	...	8	Minute; dull brown.	P
45–46	*Corticaria* spp. (2)	...	2	...	...	...	...	...	...	2	Minute; inconspicuous brownish colouring.	P
	MYCETOPHAGIDÆ.											
47	*Typhæa stercorea* L.	...	1	...	...	...	...	...	...	1	Small; dull brown.	P
	COCCINELLIDÆ.											
48	*Chilomenes lunata* F.	...	...	...	1	3	...	...	...	4	Very conspicuous; black, with bold yellowish spots and bands.	AA
49	*Scymnus trepidulus* Weise	...	...	...	...	1	...	...	...	1	Minute; thorax dull black; elytra brown, with dark dorsal stripe.	A
50	*Scymnus* sp.	...	...	...	...	...	1	...	...	1	Minute; black.	A
	BYRRHIDÆ.											
51	*Limnichus* sp.	...	...	...	...	...	...	...	1	1	Minute; black.	A
	HETEROCERIDÆ.											
52	*Heterocerus* sp.	...	...	...	...	...	...	...	1	1	Small: brown, with darker mottling.	P
	MELYRIDÆ.											
53	Gen. indet.	1	...	...	...	...	...	...	...	1	Small; inconspicuous colouring.	P
	ANOBIIDÆ.											
54	*Lasioderma serricorne* F.	...	...	1	...	...	...	...	...	1	Very small; dull dark brown.	P
	BUPRESTIDÆ.											
55	*Aphanisticus* sp.	...	...	...	...	1	...	...	...	1	Medium-sized, elongated; black, "unpleasant looking."	A

TABLE VII. (*continued*).

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus.* ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides*	Totals.	Remarks.	Colour-group.
	COLEOPTERA (*cntd.*).											
	ELATERIDÆ.											
56	*Heteroderes* sp.	11	...	...	...	..	...	...	...	11	Medium-sized; brown, with darker brown markings.	PP
57	*Craspedostethus* sp.	1	...	...	...	...	...	...	...	1	Small; bright green metallic colouring.	A
58	*Monocrepidius* sp.	...	...	1	...	...	...	...	..	1	Medium-sized; chocolate-brown.	P
59–60	? *Drasterius* spp. (2)	...	2	...	...	...	...	...	...	2	Small; inconspicuous; brown, with black markings.	P
	THROSCIDÆ.											
61	*Aulonothruscus* sp.	...	1	...	...	...	..	...	...	1	Very small; brown.	P
	LAMELLICORNIA.											
	RUTELIDÆ.											
62	*Adoretus fusculus* Fahr.	...	...	...	5	1	...	...	...	6	Large; dull brown.	P
63	*Adoretus* sp.	...	1	...	...	...	...	...	...	1	Large; dull brown.	P
	HETEROMERA.											
	ANTHICIDÆ.											
64	*Anthicus* sp.	...	...	1	...	...	...	...	...	1	Very small; brown.	P
	PHYTOPHAGA.											
	CHRYSOMELIDÆ.											
65	*Philopona fulvicollis* F.	...	...	1	...	...	...	...	...	1	Medium-sized; pale yellowish brown, with dark bands and spots.	A
66	*Eurydemus geniculatus* Jac.	...	...	...	...	1	...	...	...	1	Small; chestnut-brown.	A
67	*Luperodes quaternus* Fairm.	...	1	...	...	2	...	...	...	3	Small; inconspicuous colouring.	P
68	*Pachnephorus conspersus* Gerst.	...	8	5	1	9	...	...	...	23	Small; dark brownish grey.	P
69	*Chætocnema* sp.	...	1	1	2	3	...	...	...	7	Minute; dark brown, with dull bronze sheen.	PP
70	*Chætocnema* sp.	...	1	...	...	...	...	...	...	1	Minute; inconspicuous, brown.	P
71	*Monolepta pauperata* Er.	...	1	...	...	...	...	...	...	1	Small; straw-coloured, with brown markings.	A
72	*Monolepta* sp.	...	1	...	...	...	...	...	...	1	Small; straw-coloured.	P
73	*Aphthona* sp.	...	1	...	...	...	...	...	...	1	Small; polished dark brown.	A
	RHYNCHOPHORA.											
	CURCULIONIDÆ.											
74	*Apion* sp.	1	...	...	...	3	...	...	...	4	Very small; procryptic; greenish-grey or brown.	PP
75	*Cylas compressus* Hartm.	...	...	1	...	...	...	...	...	1	Medium-sized; dull, dark brown.	P
76	*Calandra oryzæ* L.	...	...	1	...	1	...	...	...	2	Small; dark brown.	P
77	*Isaniris* sp.	...	...	1	...	...	...	...	...	1	Small; procryptic; greyish stone colour, speckled with green.	PP
78	*Tychius* sp.	...	1	...	...	...	...	...	...	1	Small; inconspicuous, greyish-brown, with darker markings.	PP

TABLE VIII.

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Totals.	Remarks.	Colour-group.
	DIPTERA.											
	NEMATOCERA.											
	MYCETOPHILIDÆ.											
79	*Sciara stigmatopleura* Edw.	..	...	...	...	3	...	...	...	3	Small; inconspicuous, or obscurely coloured.	P
80	*Sciara leucocera* Kieff.?	...	...	1	...	8	...	...	...	9	„ „ „ „	P
81	*Sciara* sp.	...	1	...	1	2	...	...	...	4	„ „ „ „	P
82	*Platyura* (*Xenoplatyura*) sp.	...	...	...	...	1	...	...	...	1	„ „ „ „	P
	CULICIDÆ.											
83	*Ficalbia malfeyti* Newst.	...	...	...	...	...	...	.	1	1	„ „ „ „	P
84	*Culex* sp.	...	...	2	1	3	...	...	...	6	„ „ „ „	P
85	*Anopheles* sp.	...	1	...	...	...	...	...	...	1	„ „ „ „	P
86	*Mimomyia* sp.	...	...	1	...	...	...	...	...	1	„ „ „ „	P
87	*Tæniorhynchus africanus* Thes.	...	...	...	...	2	...	...	...	2	„ „ „ „	P
88	*Tæniorhynchus* sp.	...	...	...	...	1	...	...	...	1	„ „ „ „	P
	CHIRONOMIDÆ.											
89–92	*Chironomus* spp. (4)	...	1	2	...	8	...	...	..	11	„ „ „ „	P
93	*Tanytarsus* sp.	...	...	...	...	1	...	...	...	1	„ „ „ „	P
94	Sp. indet.	...	...	...	...	...	...	...	1	1	„ „ „	P
	CERATOPOGONIDÆ.											
95–97	*Bezzia* spp. (3)	...	...	...	...	5	...	...	...	5	Small; inconspicuous, or obscurely coloured.	P
98	*Stilobezzia* sp.	...	1	...	...	3	...	...	...	4	„ „ „ „	P
99–102	*Atrichopogon* spp. (4)	...	...	...	1	10	...	...	...	11	„ „ „ „	P
103	*Forcipomyia* sp.	...	...	...	1	1	...	...	...	2	„ „ „ „	P
104	*Dasyhelia* sp.	...	...	...	...	1	...	...	...	1	Minute; black.	A
105	*Neoceratopogon* sp.	...	...	...	...	1	...	...	...	1	Small; inconspicuous.	P
	TIPULIDÆ.											
106	*Gonomyia* sp.	...	...	...	...	1	...	...	...	1	Small; inconspicuous.	P
	BRACHYCERA.											
	EMPIDIDÆ.											
107	*Elaphropeza* sp.	1	...	...	...	1	...	...	...	2	Small; inconspicuous.	P
	DOLICHOPODIDÆ.											
108	Gen. indet.	...	...	...	...	1	1	...	...	2	Small; blue and bronze metallic colouring.	A
	SYRPHIDÆ.											
109	*Eumerus* sp.	...	...	2	1	...	...	...	...	3	Large; black; abdomen banded with yellow; mimetic of Hymenoptera.	AA
	MUSCIDÆ.											
110	*Musca autumnalis* de Geer?	...	1	1	2	30	...	...	...	34	7–8 mm.; thorax grey, with darker stripes; abdomen grey or yellow.	P
111	*Musca* sp.	...	4	...	...	...	2	...	...	6	6–7 mm.; obscurely coloured.	P
112	*Morellia* sp.	...	...	1	...	6	...	...	...	7	6–7 mm.; thorax blue-black, with grey stripes; abdomen blue-black.	P
	SARCOPHAGIDÆ.											
113	*Sarcophaga* sp.	...	...	...	...	3	...	...	..	3	11–12 mm.; thorax grey, with black stripes; abdomen black and grey.	P
114	Gen. indet.	1	...	...	...	...	...	...	...	1	12 mm.; grey, with black markings.	P

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides*	Totals.	Remarks.	Colour-group.
	DIPTERA (*cntd.*).											
	ANTHOMYIIDÆ.											
115–116	*Atherigona* spp. (2)	...	...	1	...	4	...	...	...	5	4 mm.; greyish thorax; abdomen yellowish-brown.	P
117–118	*Cœnosia* spp. (2)	...	...	...	...	2	...	...	...	2	4–5 mm.; thorax grey, unmarked; abdomen grey, narrowly striped with yellow.	P
119	*Limnophora* sp.	...	...	...	...	3	...	...	...	3	4–5 mm.; inconspicuous; grey and black.	P
	ORTALIDÆ.											
120	Gen. indet.	...	...	...	...	1	...	...	...	1	Small; obscurely coloured.	P
	DROSOPHILIDÆ.											
121–122	*Drosophila* spp. (2)	...	...	...	...	3	...	...	...	3	Pale brown; small.	P
123	*Drosophila* sp.	1	...	1	1	1	...	...	...	4	Pale brown; small.	P
	CHLOROPIDÆ.											
124–127	Gen. indet. (spp. 4)	...	...	...	...	6	...	...	...	6	Small; inconspicuous.	P
	AGROMYZIDÆ.											
128	Gen. indet.	...	...	...	...	1	...	...	...	1	Small; inconspicuous.	P
	DIOPSIDÆ.											
129	*Diopsis* sp.	...	...	...	1	...	...	...	...	1	Small; black, or black and red?	A

TABLE IX.

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Totals.	Remarks.	Colour-group.
	HYMENOPTERA.											
	TENTHREDINOIDEA.											
	TENTHREDINIDÆ.											
130	*Athalia* sp.	...	1	...	...	...	..	...	...	1	Large; black and yellow, with black-ringed yellow legs.	AA
	ICHNEUMONOIDEA.											
	ICHNEUMONIDÆ.											
131	*Bassus lætatorius* F.	...	...	...	...	1	...	...	...	1	Large; head and thorax black; abdomen brown and black.	A
132	*Metopius* sp.	...	...	...	...	1	...	...	...	1	Large; head and thorax black; abdomen banded black and white.	AA
	BRACONIDÆ.											
133	*Microbracon* sp.	...	...	...	...	1	...	...	...	1	Medium-sized; yellowish-brown.	A
134	*Rhogas* sp.	1	...	...	...	...	...	...	...	1	Medium-sized; yellowish-brown.	A
	CHALCIDOIDEA.											
	CHALCIDIDÆ.											
135	*Antrocephalus* sp.	...	...	1	...	...	...	...	...	1	Medium-sized; black.	A
	EURYTOMIDÆ.											
136	*Eurytoma* sp.	...	...	...	...	1	. .	...	...	1	Medium-sized; head and thorax black; abdomen dark red.	AA
137	*Eurytoma* sp.	...	...	...	...	1	...	...	...	1	Very small; black.	A
	EULOPHIDÆ.											
138	*Tetrastichus* sp.	...	...	...	...	1	...	...	...	1	Minute; black.	A

	Hyperolius marmoratus.	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Totals.	Remarks.	Colour-group.
PROCTOTRUPOIDEA.											
SCELIONIDÆ.											
139 *Hadronotus* sp.	...	...	...	...	1	...	...	...	1	Minute; black.	A
140 *Ceratoteleia mellicolor* Nixon	...	...	...	...	1	...	...	2	3	Minute; light brownish yellow.	A
141 Gen. indet.	...	...	...	...	...	...	...	1	1	Minute; black.	A
FORMICOIDEA.											
FORMICIDÆ.											
142 *Pheidole megacephala* subsp. *punctulata* Mayr.	2607	3547	1964	1115	120	24	3	552	9932	Minute; dark brown or earth-coloured.	P
143 *Monomorium subopacum* var. *australe* Emery.	2	...	...	1	1	...	...	...	4	Very small; dark brown.	P
144 *Acropyga* sp.	...	...	...	...	1	...	...	...	1	Very small; dark brown.	P
145 *Camponotus* sp.	...	...	...	...	...	...	...	1	1	Medium-sized; black.	A
VESPOIDEA.											
POMPILIDÆ.											
146 Gen. indet.	...	...	...	1	...	...	...	...	1	Medium-sized; black.	A
SPHECOIDEA.											
SPHEGIDÆ.											
147 *Notogomidia* sp.	...	...	...	...	1	...	...	...	1	Large; black.	AA
APOIDEA.											
ANDRENIDÆ.											
148 ? *Nomia* sp.	1	...	...	...	...	...	...	...	1	Medium-sized; blackish-brown; abdomen banded with yellow.	A
149 ? *Nomia* sp.	...	...	...	2	...	...	...	...	2	Large; blackish-brown abdomen; banded with yellow; pubescent.	A

TABLE XII.

Sp. No.		*Hyperolius marmoratus.*	*Hyperolius bayoni.*	*Hyperolius argus*, ♂♂.	*Hyperolius argus*, ♀♀.	*Megalixalus fornasinii.*	*Megalixalus brachycnemis.*	*Leptopelis johnstoni.*	*Phrynobatrachus acridoides.*	Totals.	Remarks.	Colour-group.
	ARACHNIDA.											
	ARANEIDA.											
150	*Clubiona annuligera* Lessert.	...	2	...	1	...	...	...	...	3	Medium-sized; cephalothorax pale brown, abdomen greenish-brown.	P
151	*Nemoscolus cotti* Lessert	...	...	2	...	...	...	...	...	2	Small; greenish-grey, legs buff, banded darker brown.	PP
152	*Dictyna montana* Tullgren?	...	...	...	4	3	...	...	...	7	Small; very procryptic; silvery-brown, with green markings.	PP
153	*Theridion blandum* Cambridge.	...	...	...	...	2	...	...	...	2	Small; yellowish-brown, with darker abdominal marks.	PP
	?	1	1	...	...	1	...	...	...	3	Medium-sized; straw-coloured.	P
	?	...	...	4	...	...	...	...	...	4	Small; straw-coloured.	P
	?	...	...	1	...	...	...	...	...	1	Medium-sized; brown and greenish-brown.	P
	?	1	...	...	...	...	...	...	...	1	Small; brown, with greenish markings.	P
	?	...	...	1	...	...	...	...	...	1	Large; brown.	P
	?	1	...	...	...	...	...	...	...	1	Medium-sized; light brown, with darker streaks and mottling.	PP
	?	...	...	...	1	...	...	...	...	1	Small; greenish-brown, with white abdominal spots.	PP
	?	...	...	...	...	1	...	...	...	1	Small; whitish, mottled with greenish-brown above, sides dark.	PP

Odonata.

Dragonflies are extremely active and watchful insects, quick to perceive approaching danger, and rapid in their take-off from rest. It is perhaps surprising to find that small tree-frogs manage to prey successfully upon them, especially when one considers the relatively large size and diffuse shape of a dragonfly, which cannot be seized and swallowed at a gulp as in the case of the conveniently small beetles, flies, bugs, and ants which mostly comprise the food of these forms. The success shown by M. fornasinii in capturing elusive prey has been mentioned on pp.8,9. Of twelve dragonflies recognized from stomach-contents, ten were recovered from this species. Unfortunately, this material was very fragmentary, and useless for further identification.

Orthoptera.

Orthopterous insects or their remains were found in all species examined except M. brachycnemis. However, on referring to Table V ., p.51 , it is at once evident that the greater part of this material was recovered from two species, namely, M. fornasinii and females of H. argus, which account for twenty-two and fifteen insects respectively

As regards coloration, all species are more or less procryptic. Earwigs (16), recovered from five species of frogs, are eaten more than any other family. Neither these nor cockroaches, which are second in number (15), appear to be distasteful to the frogs. The eleven grasshoppers taken are, without exception, exceedingly procryptic. Most of these were recovered from M. fornasinii. Crickets were found in every species except M. brachycnemis. Like the last group, these are (as far as can be determined) all markedly procryptic forms. It is noteworthy that no brightly coloured or conspicuous insect is present in this material. Blatta germanica is the only doubtful case, but the habits of this creature are typically procryptic.

Isoptera.

This order is represented solely by two worker termites (Termes natalensis Haviland) recovered from a specimen of H. bayoni which had also been feeding upon ants (Pheidole).

Hemiptera.

Hemiptera are well represented in the material from frogs' stomachs. In none of the species examined do bugs form the main food, but numerically they come second only to ants for all species collectively, representing 5.84 per cent. of the food eaten. In two frogs, H. bayoni and M. fornasinii, bugs form a fairly important item.

(1) H. bayoni. In this species Hemiptera make up

the second largest food-item, ants taking the first place; 58 bugs were recovered from 32 out of 107 (30 per cent.) stomachs.

(2) M. fornasinii. Though they do not rank with flies in importance as a food, bugs take the first place numerically. This result is due to the contents of two individuals, whose stomachs were stuffed respectively with 146 and 138 Aphids, which are apparently an exceptional form of diet occurring in only 3 per cent. of stomachs. A total of 518 bugs, notably Delphacids and Aphids, were recovered from 72 out of 245 (29 per cent.) frogs.

677 specimens (complete or fragmentary) were recovered from all frogs examined: 670 of these were identified. This material represents 12 families and at least 23 species. In the whole of this collection the only specimens falling within the AA group are three very minute first-stage larvae of a pentatomid bug, all recovered from the stomach of a single frog (M. fornasinii).

Heteropterous bugs, especially the Pentatomidae, are notorious for the vile stenches which they emit, and most members of the group are supposed to be rendered unpalatable in this way. Very many species are further protected by warning coloration. In spite of these adaptations, Heteroptera are by no means generally immune from all enemies. Judd has shown that the Song-Sparrow eats with relish Lygus and small stinking Reduviids. He says: "I know of no insectivorous bird that does not eat Heteroptera ... The stench may protect bugs from some birds of eastern United States" (51). Bugs of this great suborder are not eaten to any extent by the tree-frogs examined. Of the bugs recovered from stomach examinations, only 29 (approx. 4 per cent.) were heteropterous. With the exception of the minute first-stage larvae, it is significant that the ill-flavoured and aposematic Pentatomidae are not represented. Of the rest, it is noteworthy that there is no single case of a typically aposematic species being eaten. The Lygaeidae, Nabidae, and Capsidae are all groups within which occur glaringly conspicuous warning colours and patterns in East African species. Thus, of the lygaeid bugs, *Aulacopeltus excavatus*, *Lygaeus furcatus*, *Oncopeltus jucundus*, and *Oxycarenus maculatus* are aposematic species wearing conspicuous patterns of red and black, orange and black, yellow and black, and white and black respectively. Similarly, *Pachynomus brunneus*, a conspicuous black insect, and *Lycidocoris mimeticus*, coloured orange and black, are East African members of the Nabidae and Capsidae. All the above, and many other aposematic East African species of a size small enough to be eaten by tree-frogs, are apparently avoided. Instead, we find that, with the exception of two species (nos. 15 and 16) whose colouring is of doubtful significance (certainly not markedly aposematic), the heteropterous bugs belong to species more or less protectively coloured.

Coming to the Homoptera, we find here a fairly important article of diet in the case of some frogs, notably M. fornasinii, in which at least 64 (26 per cent.) of the frogs with recognizable food contained Delphasids and Aphids. Unlike members of the last division, the great bulk of homopterous bugs are small and inconspicuously coloured. In some families, such as the Jassidae, protective colouring predominates. According to Judd, Jassids seem to be relished by birds, but are not habitually eaten in large quantities, although they are very abundant insects. Is it to protective resemblance that they owe this degree of immunity from attack? Only two Jassids were identified in the material from all frogs examined. Psyllidae and Derbidae are likewise represented by only one and two examples respectively. By far the most abundant is Aphis maidis Fitch. Curiously enough, the large number of Aphids recovered from stomachs occurred almost exclusively in one species - M. fornasinii. Moreover, they appear to be rarely used as food, for only eight out of 245 frogs had eaten them, the stomachs of two frogs containing more than half the total number. On the other hand, the delphacid bug Peregrinus maidis, though numerically less abundant than the last, is very generally eaten by several species, especially by M. fornasinii. This bug apparently forms the main hemipterous food of H. marmoratus, H. bayoni, H. argus, M. fornasinii, M. brachycnemis, and L. johnstoni.

Coleoptera.

Beetles do not appear to form the main food of any of the tree-frogs examined. Nevertheless these insects are very generally included in the diet of four out of seven of the species whose habits have been investigated.

(1) H. marmoratus. In this species, second to ants, beetles make up the bulk of food eaten, 28 being found in 11 out of 38 (29 per cent.) stomachs with recognizable food.

(2) H. bayoni. In this species beetles take the third place in numerical importance; 47 were obtained from 34 out of 107 (32 per cent.) stomachs.

(3) H. argus. As in the last species, beetles here are subsidiary to ants and Hemiptera; only 49 were recovered from 254 frogs examined.

(4) M. fornasinii. In this species beetles are numerically of less importance than bugs, flies, and ants; 79 were obtained from 65 out of 245 (27 per cent.) stomachs containing identifiable remains.

A total of 215 beetles or beetle-fragments were recovered from stomachs. Of these, 112 were sufficiently perfect for purposes of identification. In other cases the insects were recognized by more or less fragmentary material, notably elytra. This order is represented in the present collection of undigested food by no fewer than 19 families and by at least 44 species.

Beetles possess several means of defence against predatory enemies, such as a hard and tough integument, stinking secretions and ill flavour, formidable jaws, the habit of dropping and of "death feigning," protective resemblance, warning coloration and mimicry. Two or more of these characteristics are often combined in the same insect, endowing their possessor with a varying degree of immunity from attack. These adaptations do not occur indiscriminately or at random throughout the order. Broadly speaking, certain of the characteristics are more or less typical of certain families. Thus the strongly-built Buprestidae are extremely tough and hard in texture, and with this feature is associated the brilliant metallic (warning) colouring which is typical of the family. Carabidae, Scarabaeidae, Lycidae, Coccinellidae, and Chrysomelidae are for the most part aposematic, or at any rate conspicuous, insects, and are known to possess qualities rendering them distasteful to many enemies. Carabids on being handled emit an evil-smelling and acrid liquid from the tip of the abdomen: Coccinellidae likewise produce a pungent yellow oily fluid, as do some of the chrysomelid beetles; the Lycidae are evil smelling and highly distasteful. The brightly coloured Cicindelidae appear to be defended, not by a distasteful secretion but by their wariness and by their very active habits and rapid movement, which render them extremely difficult to capture. Others, such as the Elateridae and Lampyridae, while lacking warning coloration, are yet usually considered to be unpalatable. On the other hand, many Cerambycidae and Curculionidae are typically protectively coloured, and the "death-feigning" and procryptic habits co-operate with their colouring as a means of defence. Beetles belonging to these families are usually regarded as highly edible to insectivorous animals.

We may now consider the coleopterous food of the tree-frogs, as revealed by stomach examinations, with a view to determining what light this material throws on the usefulness of various adaptations, especially that of warning coloration, as a means of protection against betrachian enemies.

Turning first to the question of colouring, it is remarkable that out of 112 identified specimens only four belonging to one species (no. 48) come into the AA category of insects with typical warning colours. Of the coleopterous fragments (i.e., elytra) which were not identified, in no case did these include - so far as I could determine - as aposematic species. Without exception, these elytra were from small or minute brown or inconspicuous species. If, therefore, we take these into account, conspicuous, or typically aposematic, insects are represented by only 1.9 per cent. of the total. This figure, based as it is upon considerable data (the remains of 215 beetles), I believe to be not without significance.

It may next be noted that the stink-producing and conspicuous Carabidae, which in the tropics are by no means confined to the ground, many species being arboreal, are entirely absent. The conspicuous and unwholesome Lycidae, which are very numerous throughout S.E. Africa, and the distasteful Cantharidae and other members of the aposematic group with lycoid markings, are totally absent from the material examined. So are the Lampyridae, which are typically inedible, and the Lagriidae. The Cetoniidae, many of which are remarkable for their bold patterns and conspicuous colours, and which have been found to be unpalatable (64), are likewise absent. All these beetles are found on flowers or foliage, for the most part freely exposed on leaves, etc., presumably in positions readily accessibly to tree-frogs, to whom they could fall easy prey. Buprestidae are represented by a single specimen (no. 55) from M. fornasinii. The active and alert tiger-beetles, whose jerky running and rapid flight render them difficult and inaccessible quarry, are absent.

On the other hand, several (at least seven) ill-flavoured (?) chafers (Adoretus fusculus) were taken, notably by females of H. argus. It is interesting to note that, in his experiments on a captive baboon, Marshall found that Adoretus flaveolus was accepted as food (64).

Of the Coccinellidae, the material includes six specimens belonging to three species. Four specimens of this aposematic family belong to the highly conspicuous and strongly smelling Chilomenes lunata, and were recovered from three individuals of M. fornasinii and from H. argus. The remaining forms (Scymnus) are minute, and neither is conspicuous.

The case of the Chrysomelidae is less easy to bring into line with the generally accepted views of edibility. Chrysomelid beetles, while usually regarded as unpalatable on account of their stinking secretions, which are frequently combined with brilliant coloration, are represented here by a higher number both of species and of individuals than any other family. Judd regarded the protective adaptations of small chrysomelid beetles as an inefficient means of protection against birds. Of them he says: "The metallic tints that were supposed to always warn off birds are constantly disregarded, and we have many birds eating green Chrysomelids" (51). Carpenter, on the other hand, in his experiments with a monkey, found that out of thirty-one species of chrysomelid and allied beetles, nearly all of which were aposematic, "all save one were treated as more or less distasteful." (12). This family certainly does not appear to be distasteful to the tree frogs. The stomachs of three species - H. bayoni, H. argus and M. fornasinii - contained respectively 14, 10, and 15 of these insects. Yet it may be noted that 35 out of the 39 specimens belonging to identified species and genera have sombre inconspicuous colouring, and are, moreover, very small or minute forms. Of the remaining four (Nos. 65, 66, 71, & 73) which I have classified as A, only Philopona fulvicollis and Monolepta pauperata are really conspicuous, the other two being doubtful cases which may well belong to the procryptic group P; in short, only two of the beetles are undoubtedly aposematic, the large majority being more or less procryptic members of the family.

From the observations of Judd, Carpenter, and others it appears that weevils (Curculionidae), the majority of which are more or less protectively coloured, are "eminently edible" to insectivorous animals. Apart from their colouring, they are protected by a number of devices, such as falling to the ground and death-feigning. There is some difference of opinion as to the protective value of these adaptions. Judd adduces evidence in support of the view that they are of little use as a protection from birds. Weevils are eaten habitually by many birds, often in large quantities. "One can hardly say in the face of these facts that the pro:tective adaptations of these weevils is highly efficient in securing them from the attacks of birds. It seems as though birds became accustomed to discriminating between weevils and gravel-stones, and knowing how palatable weevils are, the birds seek them out, and even pass over apparantly less protected insects" (51). Now, failure of a pro:tective device is one thing; to say that it is useless in the struggle for life is altogether another; and one may well be pardoned for doubting whether the procryptic colouring and habits of these highly edible beetles are as inefficient a means of protection as some writers suppose. Nine weevils are included in the present collection, representing five species, all of which are more or less procryptic.

Diptera.

Flies, may reasonably be regarded as a highly palatable form of insect food. Moreover, they are relatively defenceless insects, usually lacking the protective and aggressive devices which defend many insects of other orders, and they must be eagerly sought after by small insectivorous animals; but, owing to their alertness and rapid flight, they are difficult to capture, and they no doubt depend mainly upon this for their safety. When one considers the active habits of these insects, and the readiness with which the larger species (Muscidae, Sarcophagidae, Syrphidae, etc.) take to the wing, it is indeed surprising to find that flies are of frequent and general occurrence in the stomachs of treefrogs such as H. marmoratus, H. bayoni, H. argus and M. fornasinii. (See table XVIII) This fact speaks highly for the skill, speed, and precision with which these small batrachians are able to leap for and secure their prey.

In the case of one species, M. fornasinii, flies constitute the main food. Numerically they are exceeded by Aphids; but, judged both by bulk and by the number of stomachs from which they were recovered, flies are conspicuously the essential food upon which this species "fills up." In all 294 specimens were recovered from 133 out of 245 (54 per cent.) stomachs. 162 of these insects were medium-sized or large flies (muscid), unfortunately for the most part too fragmentary for accurate identification.

Estimated according to frequency of occurrence in individuals of all frogs examined, dipterous insects appear to be second only to ants in popularity (see Table XVIII).

For reasons stated above, the percentage of flies perfect for identification is lower than in the case of any other order of insects tabulated in this section (i.e. Orthoptera, Hemiptera, Coleoptera, or Hymenoptera), only 46 per cent. being sufficiently preserved for this purpose. Yet it is interesting to note that the number of species is the highest recorded for any order, namely, 51, as compared with Coleptera 44, Hymenoptera 20, Orthoptera 11.

The great majority of specimens (143 out of 151) are dull coloured and more or less obscurely marked, the exceptions being notably three Syrphids, typically aposematic and mimetic of Hymenoptera. We may note in passing that the Diopsidae, of which only one specimen (aposematic) was obtained, appear to be typically aposematic flies (black, or red and black) and this is interesting in the light of the following information kindly given by Dr. Edwards, who writes that: "They differ strikingly from all other Dpitera in the exceptionally hard exoskeleton, and one might suppose this would make them distasteful."

There is no example of a typically procryptic (PP) insect in this series.

Lepidoptera

Lepidoptera, both caterpillars and adult insects, were in nearly all cases too much broken up by the process of digestion to be identifiable. There is, however, one interesting feature to be noted in the material representing this group. Of the 43 caterpillars, no hairy or spiny individual was obtained. This fact strongly supports the work of Schaeffer (III) regarding the distatefulness to frogs of hairy larvae, and there can be little doubt that, so far, at any rate, as these enemies are concerned, hairs and spines act as an efficient deterrent.

Ants

Large numbers of insects of many groups, and of other Arthropods, are known to resemble ants. The explanation of these resemblances has long been a subject of controversy, and has been as hotly disputed as any of the mimcry phenonema. The whole question - which is one for specialists with an intimate knowledge of the structure and ecology of the insects concerned -

is as complex as it is fascinating. I have no intention of going into the matter here further than is necessary to introduce certain data and observations which, it is hoped, may throw some light on one aspect of the problem. It is only through the accumulation of facts regarding the ecological relationship of the ants and their organic environment that an explanation of the phenomena can ultimately be found. In the following pages I record certain observations on the relationship between ants and their batrachian enemies.

Ant-resemblances are brought about in a variety of different ways:- coloration and marking, form and habits all take their part in completing the make-up, which is often so perfect as to deceive the experienced naturalist. These phenomena, to which is devoted a considerable literature, and which are themselves beyond dispute, present a problem which is not easy of solution, and one, moreover, which seems the more remarkable the closer it is studied. It is generally believed that the resemblance confers upon the mimic concerned some benefit. Unless we make this assumption, most of the facts of ant-mimicry are rendered entirely unintelligible, and we have to fall back upon some theory of chance resemblance which restates rather than explains them. On the other hand, the evidence of the advantages accruing from ant-resemblance is by no means always clear.

The supposed advantages differ according to the following circumstances. The various phenomena of ant-mimicry fall into two natural groups, distinct on biological grounds. In the first of these we have ant-mimicing forms which enter into direct ecological relation with the ants themselves, utilizing them as food or living as guests in the ant-communities. In such cases the supposed function of the resemblance is "to deceive the host-ant in order that the guest may either devour ants and brood, or pursue in or near the nest more peaceable occupations undisturbed by the former" (79). This type of ant-mimicry must be distinguished from that exhibited by insects which apparently enter into no direct relationship with the model. In this case it is believed that the mimic benefits by protection from the attacks of predatory enemies.

It appears, therefore, that the problem has two different aspects, in each of which the factors placing a premium on ant-resemblance are, in the main, distinct. We see that while ant-guests are believed to derive protection from the ants themselves, in the case of ant-mimics not directly associated with their models the benefit, if such exists, lies rather in a degree of immunity from predatory attack. In considering the predatory habits of frogs, it is essentially with the latter aspect of myrmecoidy that we are concerned.

"The necessary support for the more popular theory that myrmecoidy serves to protect its exponents from predaceous enemies in general rather than from the ants themselves, lies in a demonstration that ants are immune from the attacks of predaceous enemies to a sufficient extent to render such relative immunity worth sharing" (79). Have we any right to assume that ants are defended from insect-eating enemies to such an extent as to endow their mimics with a degree of immunity from attack that will carry selective value? The question turns on the relationship between the ants themselves and their natural enemies, and it is one which cannot be settled until an immense amount of field-work has been done to reveal these complex relationships.

There is at present a good deal of disagreement as to the class of enemies against which the offensive and defensive adaptations of ants are effective. In the first place, it is held by McCook, Pocock, Hingston, and others that ant-mimicry is valuable as a protection against predaceous Arthropods, as opposed to vertebrate enemies. Pocock (92) says, "The unavoidable conclusion that these insects ants are palatable is rather surprising in view of the frequency with which ants of different kinds are mimicked in the tropics by Orthoptera, Coleoptera, and other insects, as well as by spiders. Nevertheless, it corroborates the opinion put forward by McCook, and amplified and endorsed by myself in 1909, before these experiments were made, that ant-mimicry is mainly serviceable as a protection against the predatory Hymenoptera of the family Pompilidae, which provision their nests with Arthropoda of various kinds, excepting ants, and are certainly the direst enemies that spiders possess." Hingston (48), in his interesting paper entitled "Field Observations on Spider Mimics," supports this view. Of the digger and mason wasps he says that they persistently prey upon spiders, which they "hunt relentlessly, pursuing them under leaves and broken bark, or driving them from tunnels in the ground. In the tropics myriads are captured in this way and carried off to provision-cells." But ants are rarely attacked by the wasps. "This being so, it is reasonable to conclude that the mimicry has a protective value, the protection being mainly from parasitic wasps."

On the other hand some writers take the opposite view. Myers and Salt (79) state: "In the more general mimicry problem Poulton and others have shown that predaceous Arthropods display very little discrimination in the choice of prey. This applies to general feeders which are, of course, the only kind against which mimicry would conceivably act as a defence; for the activities of such specialized predators as many of the solitary wasps necessarily lie as far outside the range of the mimicry problem as do those of specific parasites. We therefore find considerable agreement that the devices of the mimetic insect are operative, if at all, against the attacks of vertebrate enemies."

It has repeatedly been pointed out that ants are "dangerously armed," "aggressive," "distasteful," or well defended," and that these characteristics place the group in a position of tolerable immunity from attack. There is, however, little direct evidence that ants are by any means so immune from attack as has sometimes been supposed.

No one would deny that ants are dominant insects. Moreover, as Hingston remarks, " ... they are aggressive and well armed, and often combine to make fierce assaults." I adduce evidence of assaults made by ants on batrachians on another page. But I hardly agree with the above writer when he says of ants in the tropics: "No doubt a list of the enemies of ants could be prepared. But these would be only occasional depredations ... On the whole, they suffer very little persecution."

The subject has been extensively dealt with by Bequaert in a paper entitled "The Predaceous Enemies of Ants" (9). This writer has brought together a large number of records which prove that ants form a considerable portion of the diet of many vertebrates, i.e., frogs, toads, lizards, and insectivorous birds and mammals. It is very evident from a study of the habits of frogs in the field, and from reference to the literature of the subject, that frogs and toads are important enemies of ants, which in many species comprise the main food. In some case these insects appear to be eaten almost to the exclusion of all other forms of diet, and this in tropical species living in an environment where other insects abound. Further, frogs do not confine their attentions to the small and more defenceless species, but devour them in variety - large and small, aggressive and harmless. Thus, from five species of toads collected by the American Museum Congo Expedition, no fewer than seventy-two forms of ants were obtained, including Dorylinae, Cerapachyinae, Ponerinae, Myrmicinae, and Formicinae. In the following pages numerical data regarding the ant-eating habits of East African tree-frogs are given. One can only conclude from a study of this and other data quoted below that, so far as batrachians are concerned, ants appear to be eminently edible, and their various protective devices are of little or no avail against this class of vertebrates.

One of the most striking features revealed by the investigation of stomach-contents is the high percentage of ants present in relation to other insect-food. These insects are eaten in greater numbers, and by a greater number of frogs, than any others. The following is a brief summary of the results:-

(1) Of the seven species investigated, all prey upon ants. (2) In five species, so far as my observations show, ants form by far the most important food, amounting to 98, 96, 93, 92, and 77 per cent. respectively of all food-animals eaten. (3) In at least three species over 90 per cent. of the

frogs containing recognizable food had been feeding upon ants. (4) Observations such as these would be of little value were they based upon insufficient data, but I believe that this objection is not likely to be raised in the present case. Nearly 800 frogs were examined. These yielded in all 11,428 insects and other Arthropods. Of this total, 9937, or 87 per cent. consisted of ants - mostly workers of Pheidole megacephala subsp. punctulata Mayr., a few soldiers of the same species, and a few examples of Monomorium supopacum var. australe Emery, Acropyga sp., and Camponotus sp. (5) In many individual frogs had fed upon large numbers of ants. Lack of space forbids a complete statement of results, but the following records of ants recovered from individual frogs sufficiently indicate how largely the insects are eaten in nature:- H. marmoratus: 241, 232, 187, 173, 141, 136, 135, 113, 110, 101, 96, 93, 89, 86, 82, 82; H. bayoni: 120, 116, 106, 100, 96, 92, 92, 82, 81, 80; H. argus: 62, 55, 55, 54, 49; P. acridoides: 88, 68, 68, 58.

The figures in Table XIII which is a statement of the number of frogs containing ants and of the number of ants eaten, illustrate very clearly the place which these insects occupy in the frogs' diet.

It is interesting to note that analysis of the stomach-contents yielded some indirect evidence as to the habits of the ants (Pheidole) themselves. In the stomachs of many frogs examined I was for a long time puzzled to account for what

TABLE ~~IX.~~ XIII.

Species.	Number of frogs.			Number of food-animals.		
	Number of frogs with recognizable contents.	Number of frogs containing ants.	Per cent.	Total number of insects, etc., eaten.	Number of ants.	Per cent.
Hyperolius marmoratus	38	35	92	2675	2609	98
Hyperolius bayoni	107	104	97	3688	3547	96
Hyperolius argus, ♂♂	?	?	?	2074	1964	95
Hyperolius argus, ♀♀	?	?	?	1226	1116	91
Megalixalus fornasinii	245	67	27	1119	121	11
Megalixalus brachycnemis	9	7	78	31	24	77
Leptopelis johnstoni	6	2	33	13	3	23
Phrynobatrachus acridoides	15	15	100	602	553	92

appeared to be small seeds. The source of these was at last discovered when, on opening one stomach, I found an ant with one of these seeds still grasped firmly in its jaws. Subsequently many more ants were recovered, still giving evidence in death of their harvesting activities. Dr. Macgregor Skene, who has kindly examined this plant-material, tells me that it includes grass-seeds, a grass-flower (spikelet), and a quantity of anthers from four species of grass. These anthers were found plentifully in the frogs' stomachs, always in association with ants.

The tree-frogs commonly take up their position on the stems and blades of grasses, and no doubt they occupy their leisure by picking off the passing ants as they hurry up and down the grasses gathering provisions to store in their underground nests.

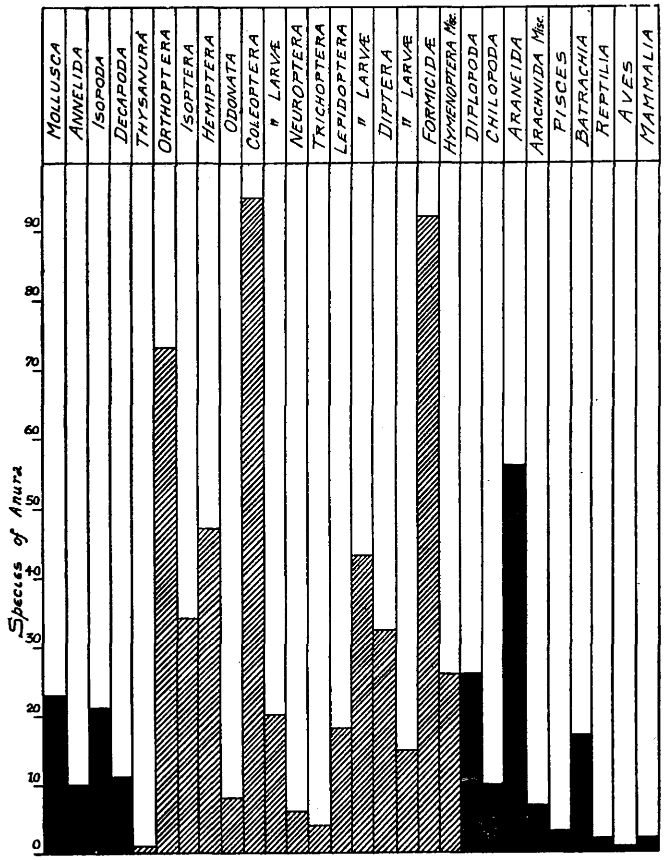
It must not be imagined, however, that the ants always fall an easy prey to batrachian enemies. Ants are aggressive insects. Though their great abundance in suitable places provides an ample source of food to those frogs which have adopted myrmecophagous habits, yet they are not obtained without a struggle. Well armed with powerful mandibles, and often with stings, ants use these weapons, or at any rate the former, to good purpose in assaulting their predatory batrachian enemies. Evidence of these attacks is afforded by ants, or the heads of ants, found attached to several frogs from the lower Zambesi. Thus one example of H. marmoratus had a worker ant (Pheidole megacephala) firmly fixed by the jaws to its foot. This individual had been feeding freely upon ants, its stomach being crammed with eighty-one of the insects. Another tree-frog (H. bayoni), whose stomach contained lepidopterous insects, one homopterous bug, one Culicid, two beetles, and fifty-two ants (P. megacephala), was found to have one of the latter still clinging to its foot after both had been killed by immersion in spirit. Loveridge (43) also mentions the hostile attacks by ants (Dorylus nigricans) on myrmecophagous Batrachia. At Nairobi a specimen of Xenopus mulleri had two soldier ants attached to it " ... as evidence of a past attack from which it had escaped victorious - amphibian war medals." Two and three ants respectively (of the same species) were found attached to specimens of Arthroleptis stenodactylus and Hemisus marmoratum from Kilosa. Barbour and Loveridge (4) record these insects as enemies of Rana adspersa and R. nutti, describing an attack on one of the latter by "about 56 small black ants." At Charre my collection of batrachians and reptiles suffered many losses from the attacks of small red ants, which, as had been mentioned elsewhere (15), would on occasion swarm into the cages containing snakes, lizards, etc., and play havoc with the reptiles. There is no doubt that the ants attacked the living animals; this was a matter of actual observation.

Now, in spite of their aggressive habits, their combined assaults and powers of defence, there is little evidence that the defences of ants are in the least degree effective against the predatory attacks of batrachians. We have already shown that they constitute the main food of H. marmoratus, H. bayoni, H. argus, M. brachycnemis, and P. acridoides. It is not unlikely that if the predatory habits of allied species are examined, we shall find a similar state of affairs. Unfortunately, little work has been done in this connection.

Wishing to ascertain how the above facts fall in line with the observations of other writers, I have collected records of frogs' feeding-habits. Owing to the difficulty of tracing references to the subject, and to the inaccessibility of certain publications, no claim is made that the list of papers referred to exhausts the recorded accounts of food-habits in frogs and toads. But I have, so far as I am aware, traced all the more important observations. Records have been included from the following sources:- Agharker (1), Barbour and Loveridge (4), Beebe (7), Bequaert(9) , Budgett (10), Chibber (13), Drake(30) , Force(35) , Frost (36), Garman(38) , Gold-smith(39) , Haber(40) , Hamilton(41) , Harrison (44), Heller (46), Hinckley(47) , Hodge(50) , Kirkland(52) , Leslie(54) , Loveridge (58) , Miller (72) , Mullan (77) , Needham(81), (82), Noble (84),(86) ,(87) , Pack (89) , Power(106),(107),Ritchie(108), Rose(109), Ruthven(110), Schmidt(112), Storer(116)(117), Strecker(118),(119), Surface(121), Thompson(124), Wright(131).

It would be impossible here to deal with these references severally in any detail. Accordingly, in text-fig. 6 I have condensed the results of an examination of the collected records of batrachian feeding-habits. These embrace data relating to the stomach analyses of 153 species and to some thousands of individuals.

It will be seen on referring to this figure that we have here strong confirmation of the view stated above that, so far as frogs are concerned, ants do not enjoy, to any appreciable extent, immunity from attack. Of the species whose recorded habits are incorporated above, 91, or about 60 per cent., Text-figure 6,



The food-habits of 153 species of Anura, showing the number of species recorded as feeding upon different groups of food-animals.

are known to eat ants. These insects are, in fact, only surpassed in popularity by the whole order Coleoptera.

In many cases the observations on feeding-habits are based on a limited number of stomach examinations, and it might be argued that the records of ants represent only occasional depredations. This may well be so, but the same argument is applicable to any other insect group, and we still have to account for the high proportion of these insects present.

On the other hand, it is equally evident , from a study of the more detailed records of Loveridge, Noble, Surface, Schmidt, Beebe, and others, that while ants are included in a high percentage of the species examined, they also, in many cases, represent the main food eaten.

Hymenoptera (other than Ants).

Hymenoptera (other than ants) are seldom accepted as food. In the present material only twenty specimens were recovered. This is less than .18 per cent. of the food eaten. When one considers the abundance of hymenopterous insects in nature, so low a percentage is significant, and furnishes additional evidence - if such is wanting - that these insects are well defended from the assault of predatory enemies.

The place which they occupy as a food of the tree-frogs examined is indicated in Table XIV.

TABLE ~~XI.~~ XIV.

Species.	Number of frogs.		Number of food-animals.	
	Number of frogs containing Hymenoptera.	Per cent.	Number of hymenopterous insects.	Per cent.
Hyperolius marmoratus	3	7·9	3	·11
Hyperolius bayoni	1	·9	1	·03
Hyperolius argus, ♂♂	?	?	1	·05
Hyperolius argus, ♀♀	?	?	3	·25
Megalixalus fornasinii	8	3·3	9	·80
Megalixalus brachycnemis	0	·0	0	·00
Leptopelis johnstoni	0	·0	0	·00
Phrynobatrachus acridoides	2	13·0	3	.50

We may note in passing that, as regards this order, _M. fornasinii_ is the least discriminating (or boldest ?) species, accounting for nearly half the insects recovered. Yet even in this species, where Hymenoptera (other than ants) reach a maximum, they make up less than 1 per cent. of the prey. Another interesting fact is that, with the exception of one frog (_M. fornasinii_) which contained two specimens, in no instance do we find more than one of these insects in any single stomach.

The order (excluding ants) is represented by ten families and by sixteen species. The latter are in every case more or less aposematic, and four species - _Athalia_ sp., _Metopius_ sp., _Eurytoma_ sp., _Notogomidia_ sp. - come definitely within the "AA" group, being relatively large and conspicuous insects.

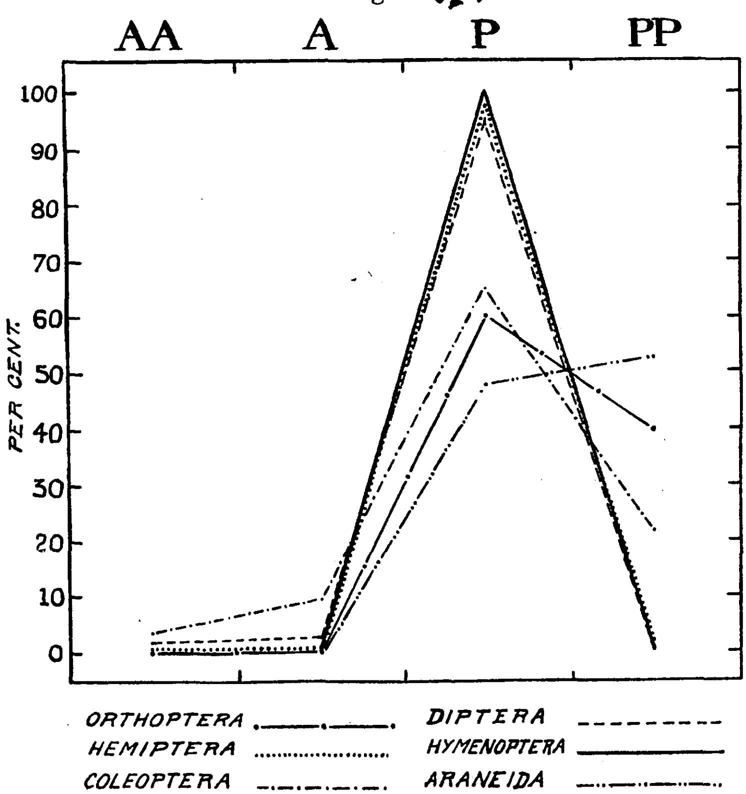
Araneida.

Spiders are represented in this material by thirty-eight specimens. In no case can they be regarded as more than an incidental item of food, occurring only in eighteen (2.2 per cent.) of the frogs examined. They belong mostly to small species, and many are immature specimens, useless for purposes of identification. All are more or less procryptically coloured.

Conclusion.

The foregoing observations are condensed in Table XV which summarises the data relating to six orders tabulated above.

Text-figure 7.



The prey of tree-frogs classified according to coloration, to show the relation between colour-habit and edibility in different orders.

TABLE XV.

Colour group.	Orthoptera.	Hemiptera.	Coleoptera.	Diptera.	Hymenoptera.	Araneida.	Total.
AA	0	3	4	3	4	0	14
A	0	3	11	4	16	0	34
P	31	650	73	144	9937	13	10848
PP	21	13	24	0	0	14	72

These figures, which are plotted in text-fig. 7 , not only furnish evidence in regard to the significance of colour and pattern in relation to edibility, and to the power of discrimination in tree-frogs; they also lend support to the argument in favour of the efficiency of common warning colours and mimicry as a means of defence. It is a striking fact that of 10,968 food-animals examined, only 14 (.13 per cent.) belong to the typically aposematic group "AA."

ii. Tree frogs from Gran Canaria.

Isopoda.

47 woodlice were recovered from 23 (12.5 per cent.) of the frogs containing recognizable food. These figures differ markedly from those recorded for tree-frogs from the Lower Zambesi, where only 4 woodlice were found in the stomachs of 798 frogs examined.

Amphipoda.

Amphipoda appear to be included only as a casual food item, this order being represented in the present material from the stomachs of two frogs each containing a single specimen.

Orthoptera.

Various orthopterous insects, notably certain grasshoppers, are probably the largest creatures normally eaten, though they are not apparently caught in great numbers.

Only 13 Orthoptera were recovered from 11 (6.0 per cent.) of the frogs containing recognizable food. This material represents 5 families, and includes 5 earwigs, a

TABLE ~~II.~~ XVI.

Sp. no.		Speci-mens.	Remarks.	Colour-group.
	ORTHOPTERA.			
	FORFICULIDÆ.			
1	Gen. indet.	3	Medium-sized; brown.	P
	BLATTIDÆ.			
2	Gen. indet.	1	Large; dark brown.	P
	ACRIDIDÆ.			
3	*Aulacobothrus* sp.	1	Large; light brown, with darker brown marks on legs and tegmina.	PP
4	*Acridinæ*, gen. indet.	1	Small; earth-coloured.	PP
5	*Acridinæ*, gen. indet.	1	Medium-sized; buff.	P
	TETTIGONIIDÆ.			
6	*Phaneroptera* sp.	1	Large; green.	PP
7	*Decticinæ*, gen. indet.	1	Large; light brown marked with darker brown.	PP
8	Gen. indet.	1	Medium-sized; grey, with brownish-grey marks.	PP
	GRYLLIDÆ.			
9	*Gryllus* sp.	1	Medium-sized; dark brown.	P
	HEMIPTERA.			
	HETEROPTERA.			
	CYDNIDÆ.			
10	*Macroscytus brunneus* (F.)	6	9 mm.; chestnut or dark brown.	C

TABLE XVI (*continued*).

Sp. no.		Speci-mens.	Remarks.	Colour-group.
	SCATOPSIDÆ.			
80	*Swammerdamella brevicornis* Meig. (?)	1	2 mm.; dark brown.	P
	BOMBYLIIDÆ.			
81	*Geron gibbosus* Meig.	1	5 mm.; black, with white pilosity.	A
	DOLICHOPODIDÆ.			
82	*Syntormon pallipes* Fabr.	2	3 mm.; black, with bronze and green metallic sheen.	A
	CYCLORRAPHA.			
	AGROMYZIDÆ.			
83	*Liriomyza pectoralis* Beck. (?)...	1	2 mm.; thorax black, abdomen dark brown, reddish on sides, legs black and yellow.	A
	DROSOPHILIDÆ.			
84	*Scaptomyza apicalis* Hardy var. *flava* Fall.	2	2 mm.; thorax yellowish brown, abdomen dark brown.	P
85	*Diastata anus* Meig. (?)	1	Minute; yellow.	C
	EPHYDRIDÆ.			
86	*Hydrellia ranunculi* Hal. (?) ...	2	2 mm.; dull brownish-black.	P
87	Gen. indet	5	Small; inconspicuous.	P
	CHLOROPIDÆ.			
88	*Chloropisca notata* Meig..........	1	Small; obscurely coloured.	P
	CYPSELIDÆ.			
89	*Scatophilella* (*Limosina*) *heteroneura* Hal.	1	Minute; black.	P
90	*Cypsela* sp.	2	4 mm.; black.	C
91	*Leptocera* sp........................	4	2 mm.; black.	C
92	*Rachispoda limosa* Fall. (?)	1	2 mm.; dull black.	C
	CHAMÆMYIIDÆ.			
93	*Parochthiphila spectabilis* Löw. (?)	1	2·5 mm.; grey, legs yellowish.	P
	SEPSIDÆ.			
94	*Sepsis violacea* Meig.	2	4 mm.; black, with violet sheen; waisted, resembling Hymenoptera.	AA
95	*Sepsis cynipsea* Meig.	1	Small; shining black.	A
96	*Sepsis* sp.	1	Small; black.	A
	PIOPHILIDÆ.			
97	*Piophila casei* Linn. (?)	1	3·5 mm.; black.	C
	SCIOMYZIDÆ.			
98	*Sciomyza pallidiventris* Fall. (?).	1	4 mm.; greyish brown.	P
	MUSCIDÆ.			
99	*Limnophora* sp.....................	1	4–5 mm.; grey-brown, inconspicuous.	P
100	*Fannia scalaris* Fabr.	1	6–7 mm.; greyish black.	C

XVI

TABLE ~~II~~. *(continued)*.

Sp. no.		Specimens.	Remarks.	Colour-group.
	PENTATOMIDÆ.			
11	*Sciocoris sideritis* Woll.	1	5 mm.; greyish brown.	P
	LYGÆIDÆ.			
12	*Noualhieria quadripunctata* (Brullé).	13	7 mm.; dark brown, with four white spots.	A
13	*Heterogaster artemisiæ* Schill....	3	5 mm.; chestnut and dark brown.	P
14	*Aphanus alboacuminatus* (Goeze).	1	5·5 mm.; dark brown, black and white.	A
15	*Beosus maritimus* (Scop.)	1	6 mm.; light brown, with dark and light marks.	C
16	*Dieuches armipes* (F.)	1	11 mm., dark brown, with lighter marks.	C
	PYRRHOCORIDÆ.			
17	*Scantius ægyptius* (L.)	1	9 mm.; red and black; highly conspicuous.	AA
	HEBRIDÆ.			
18	*Hebrus pusillus* (Fail.)...........	1	2 mm.; dark brown.	P
	REDUVIIDÆ.			
19	*Reduvius personatus* (L.)	1	17 mm.; dull brownish grey.	C
	NOTONECTIDÆ.			
20	*Notonecta canariensis* Kirk. ...	1 }	17 mm.; straw-coloured, marked with brown and dark green.	{ P
21	*Notonecta* sp., larva	1 }		{ P
	HOMOPTERA.			
	CERCOPIDÆ.			
22	*Philænus angustipennis* Horv. .	2	6 mm.; straw-coloured.	PP
	JASSIDÆ.			
23	*Deltocephalus* sp.	1	3 mm.; procryptic: buff, faintly streaked with green and brown.	PP
24	*Limotettix* sp.	1	2·5 mm.; inconspicuous, greenish grey.	PP
	APHIDIDÆ.			
25	*Rhopalosiphum* sp.	1	Minute; inconspicuous.	P
	COLEOPTERA.			
	CARABOIDEA.			
	CARABIDÆ.			
26	*Bembidium atlanticum* Woll....	1	6 mm.; dark brown.	C
27	*Bembidium subcallosum* Woll. .	3	4 mm.; polished dark brown, with two lighter spots.	C
28	*Trechus flavolimbatus* Woll. ...	2	3 mm.; brown.	P
29	*Tachys curvimanus* Woll.	1	2·5 mm.; light buff.	P

TABLE ~~II~~ XVI (*continued*).

Sp. no.		Speci-mens.	Remarks.	Colour-group.
	HALIPLIDÆ.			
30	*Haliplus suffusus* Woll.	1	4 mm.; inconspicuous.	P
	GYRINIDÆ.			
31	*Gyrinus striatus* F.	1	7 mm.; metallic colouring green and black, elytra with yellow marginal stripe.	A
	STAPHYLINOIDEA.			
	STAPHYLINIDÆ.			
32	*Aleochara nitida* Grav.	1	4 mm.; brownish black.	C
33	*Boletobius* sp.	1	4 mm.; brown.	P
34	*Philonthus nigritulus* Grav. ...	4	4 mm.; dark brown.	P
35	*Philonthus tenellus* Woll.	3	Small; dark brown.	P
36	*Platystethus cornutus* Grav. ...	8	3 mm.; brown and black.	C
37	*Tachyporus nitidulus* F.	1	3 mm.; brown, inconspicuous.	P
38	*Trogophlœus bledioides* Woll. (?)	2	2·5 mm.; dark brown.	P
	TRICHOPTERYGIDÆ.			
39	*Ptenidium apicale* Gillm.	1	Minute; inconspicuous.	P
	DIVERSICORNIA.			
	COCCINELLIDÆ.			
40	*Scymnus canariensis* Woll.......	22	2 mm.; thorax black, elytra dull yellow with black spot.	A
41	*Scymnus cercyonides* Woll.......	1	Minute; light brown.	P
	PARNIDÆ.			
42	*Parnus proliferícornis* F.........	2	5 mm.; dull, dark brown.	P
	HYDROPHILIDÆ.			
43	*Hydræna* sp........................	1	Small; inconspicuous.	P
44	*Ochthebius riparius* St.	1	Minute; inconspicuous.	P
	PTINIDÆ.			
45	*Anobium velatum* Woll. (?)......	3	4 mm.; dull brown.	P
46	*Casapus alticola* Woll.............	6	4 mm.; dark brown, with light grey markings.	PP
47	*Casapus radiosus* Woll.	1	4 mm.; brown, with lighter marks.	PP
48	*Piotes inconstans* Woll.	5	Small; dark brown.	P
49	*Sphæricus* sp.	1	Minute; inconspicuous.	P
50	Gen. indet...........................	1	2·5 mm.; brown.	P
	ELATERIDÆ.			
51	*Lacon* sp.	1	12 mm.; dark brown.	P
	HETEROMERA.			
	TENEBRIONIDÆ.			
52	*Gnophota cribricollis* Brull.......	5	6 mm.; dull black.	C
53	*Gonocephalum* (*Opatrum*) *fuscum* Hbst.	2	8 mm.; dark brown.	P

TABLE ~~II.~~ XVI (*continued*).

Sp. no.		Speci-mens.	Remarks.	Colour-group.
	TENEBRIONIDÆ (*cont.*).			
54	*Gonocephalum* (*Opatrum*) *hispidum* Brull.	3	8 mm.; dull brown.	P
55	*Gonocephalum rusticum* Oliv....	1	9 mm.; dull, dark brown.	P
56	*Hegeter impressus* Brull.	2	12 mm.; dull black.	A
57	*Melansis costatus* Brull.	9	8 mm.; dull black.	C
58	*Opatropis hispida* Brull.	2	7 mm.; dull, greyish-brown	P
59	*Scleron asperulum* Woll.	2	7 mm.; earth-coloured.	PP
	ŒDEMERIDÆ.			
60	*Ditylus concolor* Brull.	10	14 mm.; brownish-yellow.	C
	ANTHICIDÆ.			
61	*Anthicus canariensis* Woll.	2	Small; light brown.	P
62	*Anthicus crinitus* Cast.	2	3 mm.; brown, with dark markings.	PP
63	*Anthicus guttifer* Woll.	3	3 mm.; dark brown, with lighter marks.	PP
	RHYNCHOPHORA.			
	CURCULIONIDÆ.			
64	*Apion rotundipenne* Woll.	1	2·5 mm.; dark brown.	PP
65	*Apion sagittiferum* Woll.	1	2 mm.; greyish brown.	PP
66	*Apion umbrinum* Woll.	1	3 mm.; dull black.	P
67	*Apion* sp.	1	Small; inconspicuous.	P
68	*Atlantis angustula* Woll.	2	7 mm.; polished, black.	C
69	*Calandra oryzæ* L.	2	3 mm.; dull, dark brown.	P
70	*Hyperstichus eremita* Oliv. ...	23	14 mm.; dull black, with green or golden bloom.	P
71	*Laparocerus compactus* Woll....	7	4 mm.; dull brown.	P
	PHYTOPHAGA.			
	BRUCHIDÆ.			
72	*Bruchus* sp.	1	Small; dull, inconspicuous.	P
73	*Bruchus brachialis* Fahrs.	1	Small; procryptic.	P
	CHRYSOMELIDÆ.			
74	*Cryptocephalus nitidicollis* Woll.	1	2·5 mm.; straw-coloured.	P
	LAMELLICORNIA.			
	APHODIIDÆ.			
75	Gen. et sp. n.	1	Small; brown, inconspicuous.	P
76	*Saprosites* sp.	1	Small; dark brown.	P
	DIPTERA.			
	ORTHORRAPHA.			
	TIPULIDÆ.			
77	*Gonomyia tenella* Meig.	1	5 mm.; light brown, inconspicuous.	P
78	*Ilisia* sp.	1	5 mm.; light brown, inconspicuous.	P
79	*Limonia* sp.	3	8–10 mm.; light brown, inconspicuous.	P

TABLE ~~II~~ XVI (*continued*).

Sp no.		Speci-mens.	Remarks.	Colour-group.
	MUSCIDÆ (*cont.*).			
101	*Chortophila radicum* Linn.	1	4 mm.; dull grey.	P
102	*Musca domestica* Linn.	1	6 mm.; grey and black.	C
103	*Musca tempestiva* Fall.	1	3–4 mm.; grey-black.	C
104	Gen. indet.	10	Indet.	
	LARVÆVORIDÆ.			
105	*Stomorhina lunata* Linn.	1	6 mm. grey and black.	C
	HYMENOPTERA.			
	ICHNEUMONOIDEA.			
	ICHNEUMONIDÆ.			
106	*Pimplinæ*, gen. indet.	2	Medium-sized; black and brown.	A
107	*Cryptinæ*, gen. indet.	1	Medium-sized; conspicuous.	A
108	*Ophioninæ*, gen. indet.	1	Medium-sized; dull chestnut.	C
	BRACONIDÆ.			
109	*Blacus* sp.	1	Minute; brown.	P
	CYNIPOIDEA.			
	FIGITIDÆ.			
110	*Eucoila* sp.	1	Small; brown and black.	A
	FORMICOIDEA.			
	FORMICIDÆ.			
111	*Pheidole* (*Pheidole*) *megacephala* F.	2	3 mm.; brown.	P
112	*Monomorium subopacum* Smith.	15	2 mm.; dark brown.	P
113	*Solenopsis fugax* Latr.	2	3 mm.; black.	C
114	*Leptothorax* sp.	1	3 mm.; brown.	P
115	*Messor barbarus* L. subsp. *minor* André.	3	7 mm.; dark reddish brown and black.	A
116	*Tetramorium cæspitum depressum* For.	50	4 mm.; shiny, dark brown.	C
117	*Tetramorium meridionale* Emery.	1	2 mm.; brown.	P
118	*Tapinoma nigerrimum* Nyl. ...	2	4 mm.; dark brown.	P
119	*Aphænogaster testaceopilosa* Lucas.	2	5 mm.; dull black.	A
120	*Crematogaster* sp.	5	4 mm.; shiny, brown.	C
121	*Crematogaster scutellaris* Ol. ...	76	4 mm.; shiny, brown.	C
122	*Crematogaster* sp.	60	4 mm.; shiny, brown.	C
123	*Acanthomyops* (*Donisthorpea*) *niger* L.	76	4 mm.; dark brown.	P
124	*Plagiolepis pygmæa* Latr.	7	1·5 mm.; dark brown.	P
125	*Iridomyrmex humilis* Mayr. ...	2	2 mm.; brown.	P
126	*Camponotus* (*Camponotus*) *vagus* Scop.	28	6 mm.; dull black.	A
127	*Camponotus* (*Myrmentoma*) *libanicus* André.	2	6 mm.; black.	A

TABLE ~~II.~~ XVI (*continued*).

Sp. no.		Speci-mens.	Remarks.	Colour-group.
	APOIDEA.			
	ANDRENIDÆ.			
128	*Halictus viridis* Brullé var. *unicolor* Brullé.	2	10 mm.; black, with green metallic sheen.	AA
129	*Halictus* sp.	1	10 mm.; black, with green metallic sheen.	AA
	ARACHNIDA.			
	ARANEÆ.			
	DYSDERIDÆ.			
130	*Dysdera insulana* Simon	1	7 mm.; dark brown.	P
131	*Dysdera* sp.	1	9 mm.; orange-brown.	C
	ZOROPSIDÆ.			
132	*Zoropsis rufipes* Lucas	3	13 mm.; cephalothorax light brown, abdomen brownish grey.	P
133	*Zoropsis* ? sp.	2	5 mm.; light brownish grey.	P
	DRASSIDÆ.			
134	*Leptodrassus hylæstomachi* Berland, sp. n.	1	3 mm.; light grey.	P
135	*Scotognatha convexa* (Simon)	1	Large; brown.	P
	AGELENIDÆ.			
136	*Agelena canariensis* (Lucas)	2	8 mm.; brown, abdomen greyish brown.	P
	DICTYNIDÆ.			
137	*Dictyna puella* Simon	1	3 mm.; brown, abdomen greyish brown.	P
	THERIDIIDÆ.			
138	*Teutana grossa* (C. Koch)	1	6 mm.; cephalothorax light brown, abdomen brownish grey.	P
139	*Argiopinæ*, gen. indet.	1	Indet.	
	LINYPHIIDÆ.			
140	*Lephthyphantes tenuis* (Blackwall).	4	2 mm.; cephalothorax brown, abdomen whitish, with dark brown spots.	P
	EPEIRIDÆ.			
141	*Tetragnatha nitens* (Audouin)	4	Large; elongated; cephalothorax buff, abdomen olive, closely spotted with silvery white.	PP
142	*Meta* ? sp.	2	3 mm.; cephalothorax white, with median dark brown band; abdomen dark brown, with silver markings.	PP
143	*Zilla* ? sp.	1	5 mm.; light brown, abdomen greyer with dark markings.	P

cockroach, 6 grasshoppers, and a cricket.

Of the 11 insects which are not too far digested for examination, all belong to more or less procryptic species, coloured either green or some other shade of brown, often with a disruptive pattern of darker bars or spots.

Hemiptera.

This order is poorly represented in the material examined, which includes 43 bugs, belonging to 10 families and to some 16 species, recovered from 36 (19.6 per cent.) stomachs. 36 specimens were sufficiently well preserved for purposes of identification; of these 31 belong to the Heteroptera.

Odoriferous glands are characteristic of a large number of this great suborder. Especially are the shield-bugs (Pentatomidae) notorious for the vile stenches which they emit. Associated with these nauseous qualities many species, notably among the Pentatomidae, Lygaeidae, Nabidae, and Capsidae, are decked out in a conspicuous livery of aposematic colours.

That heteropterous bugs should figure so prominently in the hemipterous food of H. arborea is therefore surprising. The actual number of Heteroptera is greater than that recorded from the stomachs of more than four times as many East African Tree-Frogs(20).

In the present material the ill-flavoured Pentatomidae are represented by a single specimen, Sciocoris sideritis Woll. On the other hand, it will be seen on referring to p. 90 that the aposematic and presumably unpalatable Lygaeidae are far from immune to attack, for no fewer than twenty bugs of this family are included in the food examined. Thirteen of these are referable to Noualhieria quadripunctata (Brulle), an aposematic (dark-brown and white) species; four of these bugs were taken from a single stomach.

The present collection contains only a single specimen classified in the AA group, namely, a Pyrrhocorid, Scantius aegyptius (L.), wearing a vigorous pattern of red and black.

Homoptera are represented by five insects only - two Cercopids, two Jassids, and an Aphid.

Coleoptera.

Beetles play an important part in the food of Hyla arborea. Whether considered numerically or in relation to the number of stomachs in which the insects occur they are second only to the Hymenoptera. When account is taken of their greater bulk as compared with the small - if more numerous - ants which largely make up the hymenopterous total, it is clear that the dominance of the latter group is more apparent than real; beetles, in actual fact, constitute the main group of food-animals.

A total of 200 specimens (complete or fragmentary) were recovered from 104 out of 184 (56.6 per cent.) frogs containing recognizable prey; 161 of these insects were sufficiently perfect for purposes of identification.

This material represents 17 families and at least 51 species. The main families preyed upon, in order of preference, are as follows:-

Curculionidae..........	8 species, 38 specimens.
Tenebrionidae..........	8 species, 26 specimens.
Coccinellidae..........	2 species, 23 specimens.
Staphylinidae..........	7 species, 20 specimens.
Ptinidae...............	6 species, 17 specimens.

It will be seen that weevils head the list with 38, or about 24 per cent. of the beetles identified. This fact is in accordance with the generally accepted view of Judd (51), Carpenter (12), and others who regard the Curculionidae as "eminently edible" and much sought after by insect-eaters. In this connection it may be mentioned that Beal, referring to the food of the Hermit Thrust (Hylocichla guttata), of which 68 stomachs were examined, records beetles as making up 11 per cent. of the food. More than two-thirds of these beetles consisted of weevils (U.S. Dept. of Agric., Biol. Survey, Bull. 30, 1907).

The great majority of beetles eaten belong to species more or less inconspicuous in nature. In the whole collection there is not one beetle of medium or large size referable to the AA class.

Of the ground-beetles and ladybirds, four species of the former (Carabidae) and two of the latter (Coccinellidae) are included in the tree-frogs' menu. Members of both these families secrete evil-smelling fluids which render them relatively unpalatable to many enemies. The above carabids (nos. 26-29), none of which belongs to aposematic species, are small beetles not exceeding 6 mm. in length, and it appears that such forms are less efficiently protected than the larger stink-producing ground-beetles; for in this connection Judd (51) states that "the smaller Carabidae, whether stinking or not, are eaten by practically all land-birds."

The Coccinellid material consists of nothing more formidable than two minute species, the larger, Scymnus canariensis Woll., measuring only 2 mm., and S. cercyonides Woll., about 1 mm. in length. The former is, however, a conspicuous insect, black and dull yellow in colour, and it is perhaps surprising to find as many as 22 specimens in the food-material examined.

Only two other beetles belonging to the A group occur here, namely, A Gyrinid, Gyrinus striatus F., whose colour-scheme is of doubtful significance, and a dull black Tenebrionid, Hegeter impressus Brull.

Finally, the Chrysomelidae, generally regarded as relatively unpalatable on account of their stinking secretions, are represented by one example of a small inconspicuous species - Cryptocephalus nitidicollis Woll.

Diptera.

As we have pointed out elsewhere, flies - if only they can be caught - make satisfactory and digestible fare. Lacking the protective and aggressive devices, such as a hard or leathery exoskeleton, stinking secretion, sting or powerful mandibles which defend many insects of other orders, flies depend for safety upon alertness and rapid flight. The difficulty of capturing such active prey probably accounts for the fact that only 74 flies were found in the stomachs examined. These insects, representing no fewer than 15 families and 29 species, were recovered from 33 (17.9 per cent.) of the frogs.

Of 42 specimens perfect enough for identification, the great majority are dull-coloured and more or less obscurely marked. The exceptions are five fairly conspicuous (A) species belonging to the Bombyliidae (no. 81), Dolichopodidae (no. 82), Agromyzidae (no. 83), and Sepsidae (nos. 95, 96), and two examples of the hymenopterous mimic Sepsis violacea Meig. - the only typically aposematic (AA) fly in the series.

Neuroptera.

This order is represented solely by fragmentary remains of two insects, namely, a hemerobiid (?) larva and a myrmeleonid.

Lepidoptera.

Caterpillars and adult Lepidoptera rapidly become broken up by the powerful gastric juices of Anura. In the present collection of food-animals the recognized débris of 13 imagines and 24 caterpillars recovered from 27 frogs contained scarcely any material that could be identified.

Dr. E. A. Cockayne, who kindly examined the caterpillar fragments, refers eight larvae to the family Noctuidae. One of these "belongs to one of the genera nearly allied to *Heliothis*," probably to *Heliothis* or *Chloridea*. Another was identified as belonging to the genus *Plusia*. Of the remainder all that could be recognized were "two undoubted micro-lepidoptera, ? Tortricidae."

Ants.

Much has been written, and many have been the controversies, concerning the protective adaptations of ants, their supposed relative immunity from the attacks of insectivorous animals, and the efficiency of any mimicry as a protection against predatory enemies. The relation between ants and batrachian enemies has been discussed in some detail in my earlier paper, (20, p.513). In this I showed that there is little evidence that the defences of ants are in the least degree effective against the predatory attack of many Anura; that ants are eaten by a greater number of anuran species than any other group of insects except the Coleoptera; that many species feed upon ants almost to the exclusion of all other food; and that frogs, toads, and tree-frogs probably rank among the most important enemies of the Formicidae.

The figures recorded below for the Canary Island Tree-Frog lend additional support to these conclusions.

Out of 1210 food-animals, 695 were ants. Representing 57.4 per cent. of the food, this collection is more than three times the number recorded for any other single order of insects. That ants are very generally eaten by Hyla arborea is shown by their distribution in the stomachs of 136 out of 184 (74.0 per cent.) frogs containing recognizable prey.

Seventeen species are recorded (nos. 111-127); these range from small forms such as Pheidole (Pheidole) megacephala F., Plagiolepis pygmaea Latr., and Iridomyrmex humilis Mayr., to large formidable species like Camponotus (Camponotus) vagus Scop.

Hymenoptera (other than Ants).

Hymenoptera (other than ants) appear to be relatively unacceptable to the frogs. In this respect the figures relating to the hymenopterous food of the present species recall those recorded for East African Tree-Frogs. In both cases ants are very numerous, while other hymenopterous insects are remarkably scarce. Thus we find here besides the ants only 9 specimens, namely, 4 ichneumons, a braconid, a cynipid, and 3 bees. These represent 0.74 per cent. of the food eaten - a figure significantly low, and out of all proportion to the abundance of the group in nature.

Araneae.

Spiders appear here as a fairly popular food-item. The group is represented by 70 specimens derived from 54 (29.3 per cent.) frogs containing recognizable food. These figures contrast strikingly with those recorded for various tree-frogs of the Lower Zambesi, where only 38 spiders were recovered from 18 out of 467 (3.9 per cent.) frogs with recognizable prey, and where the percentage containing spiders in the case of the four species most thoroughly investigated is as follows:- Hyperolius marmoratus (5.3 per cent.), H. bayoni (4.7 per cent.), H. argus (2.1 per cent.), Megalixalus fornasinii (3.7 per cent.).

Among the Zambesi collection was one spider, Nemoscolus cotti Lessert * hitherto undescribed, and now once again a tree-frog has eaten a species new to science. The description of Leptodrassus hylaestomachi, sp. n., by Monsieur Berland appears in P.Z.S. 1934, p. 423.

* Lessert, R. de. 1933. Araignées d'Angola, Reine Suisse de Zoologie, xl, p. 109.

Unfortunately much of the present material was in a bad condition, and therefore useless for systematic purposes; moreover, many specimens were immature. In this connection Monsieur L. Berland, who kindly studied the collection, writes "generally only adult specimens of Spiders may be studied, and of course frogs don't take care of this fact!"

24 specimens, representing 8 families and 14 species, were tolerably well preserved. As regards coloration all, with one doubtful exception (no. 131), are more or less procryptic. In this respect they agree with the East African Tree-Frogs' spider prey, all of which fall within the procryptic classes P and PP.

The dominance of concealing coloration is not surprising when one considers that although spiders have venom of sufficient strength to enable them to overcome the animals upon which they habitually prey, their poisonous qualities can rarely protect them from predatory enemies. In other words, considered as a group spiders are defenceless and much sought after for food by a host of enemies. They are relentlessly persecuted by various wasps (Pompilidae, Sphegidae), and by Ichneumonidae; they are preyed upon by certain flies (Asilidae), by dragonflies, and by beetles (Cicindelidae); they are devoured by a multitude of small insectivorous vertebrates, including frogs, toads, and tree-frogs, salamanders, lizards, monkeys, and shrews, and especially by birds. Of the last group alone McAtee records more than 300 Nearctic species feeding upon spiders.

Having, therefore, no direct protection from such enemies, the chief defences of spiders consist in various devices for concealment, ranging from death feigning, dropp-ing from the web, concealment in burrows, simple procryptic coloration and flash colours to the construction of compli-cated special devices "such as pellets, bands, spirals, zigzags with which they blend when seated in their snares."(48) The variety and elaboration of these camouflage schemes sufficiently indicate the dire need which spiders have of concealment from their predatory and parasitic foes, and the dominance of protective coloration in the group recalls the case of Curculionid beetles, which, being likewise both palatable and much sought after by birds and other insecti-vorous animals, also combine dropping and death-feigning instincts with the procryptic colouring so typical of this great family.

Acarina.

Of the nine mites, recovered from eight stomachs, those which were sufficiently well preserved have been determined by Dr. Finnegan as follows:-

Anystidae:	*Anystis baccarum* (Linn.)
Trombidiidae:	*Trombidium* sp.
Oribatidae:	*Oribata orbicularis* (Koch)
Laelaptidae:	*Hypoaspis* sp.

Mites are probably the smallest prey normally taken by *Hyla arborea*, and they can at best be scarcely worth the trouble of picking up.

Chilopoda.

Myriapoda appear to be little eaten by tree-frogs. Not one specimen was found among 11,428 food-animals recovered from the Zambesi tree-frogs. In the present collection are included the remains of nine small centipedes, all of which appear to be Geophilids. Millipedes are absent.

Conclusion.

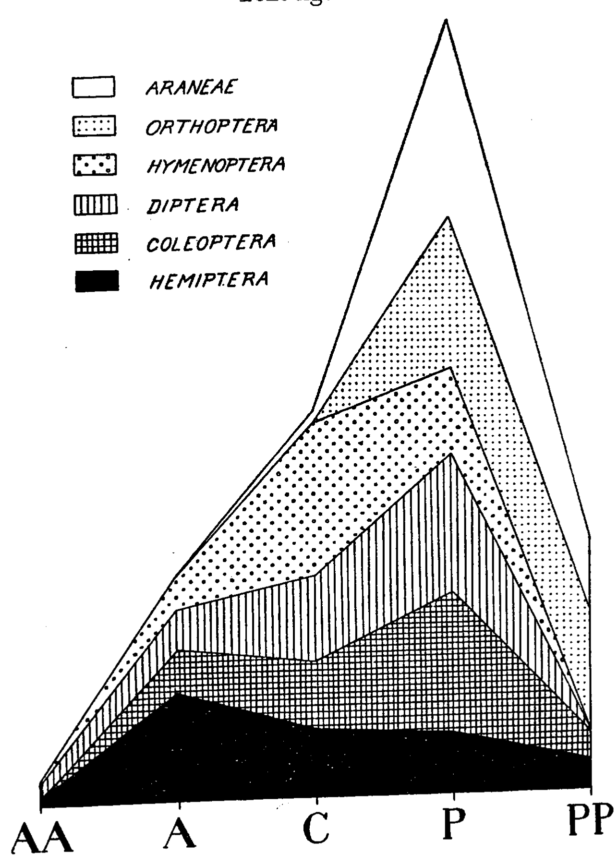
The foregoing observations are condensed in Table XVII which summarizes the data relating to Orthoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, and Araneae.

Table XVII.

Colour-group.	Orthoptera.	Hemiptera.	Coleoptera.	Diptera.	Hymenoptera.	Araneæ.	Total.
AA	0	1	0	2	3	0	6
A	0	14	25	6	39	0	84
C	0	9	39	13	194	1	256
P	6	8	81	21	107	17	240
PP	5	4	16	0	0	6	31
Total	11	36	161	42	343	24	617

These figures are shown graphically in text-fig. 8 which illustrates the percentage distribution of food-animals according to colour-groups for each of the above orders. They furnish interesting evidence in regard to the significance of colour in relation to edibility. The bearing of this type of evidence on the theory of warning colours and mimicry has been discussed in my earlier paper (20, p.523). It is only necessary here to point again to the low percentage of aposematic animals in the frogs' food. Out of 617 specimens critically examined six belong to the typically aposematic group "AA".

Text-figure 8.



These figures agree with those based upon the colour-classification of the prey of East African tree-frogs in lending additional support to the existing mass of evidence upon which the theory of warning colours and mimicry depends.

3. Frogs as a Factor in the Production of Warning Colours.

i. Frogs considered as Enemies of Insects.

It may be suggested that tree-frogs and other batrachians, by reason of their (relatively) small size, as compared with insectivorous birds and mammals, do not destroy a sufficiently large amount of insect-life to justify their inclusion among the important enemies of insects. Yet I am convinced that in those parts of the tropics where batrachians abound this is far from the truth.

Frogs are voracious animals, and well adapted to the habit of eating relatively enormous meals. Kirkland, whose intensive studies of the feeding-habits of the American Toad (*Bufo lentiginosus americanus*) are referred to elsewhere, made many observations, during a period of two years, "on toads feeding under natural conditions at all hours of the night." He throws some interesting light on the vigorous appetite and no less vigorous digestion of these creatures. "In twenty-four hours," he says, "the amount of food consumed is equal in bulk to about four times the stomach capacity. In other words, the toad's stomach is practically filled and emptied four times in twenty-four hours." (52).

Abundant proof that toads and frogs are in the habit of taking meals of enormous proportions is afforded by stomach examinations of specimens freshly caught in the field. Of the frogs from the lower Zambesi collected and examined by the writer, the following stomach-contents are remarkable for their bulk:- One specimen of Megalixalus fornasinii, 37 mm. in length, contained three grasshoppers measuring (head and abdomen) 25, 21, and 21 mm. respectively. In the stomach of another individual was found the following assortment: three bugs (Peregrinus maidis), one small brown beetle, two flies (Musca), and seven small Diptera, one Ichneumon (Bassus laetatorius), one Braconid (Microbracon), and one spider. A third specimen of this species, 24 mm. in length, held in its stomach seven muscid flies, each about 7 mm. in length, and one small Dipteron; these insects were in perfect condition, and had evidently been taken immediately prior to the frog's capture. The prodigious meals taken by this species are well illustrated by the photograph (20, Pl.I,fig.1) which shows the distended stomach of a specimen of M. fornasinii before it was opened for examination. In the case of a closely allied species, M. loveridgii, Barbour and Loveridge describe an example from Derema whose stomach contained "a 20 mm. caterpillar, an 11 mm. grasshopper (head and abdomen measurement), and a 5 mm. spider." One specimen of H. bayoni, 22 mm. in length, from the Zambesi collection, contained a muscid fly, and a caterpillar measuring 24 mm. In the case of *H. marmoratus*, one much swollen stomach was stuffed with six homopterous bugs (*P. maidis*), two beetles, three dipterous insects (Culicids ?), forty-four ants (*Pheidole megacephala*), and one Braconid (*Rhogas*).

Other evidence of the prodigious meals taken by frogs, toads, and tree frogs in nature is presented and discussed elsewhere (Cott, 20, pp. 526-528).

Mention has been made (Cott, 20 , pp. 474, 490) of the great abundance of tree-frogs in the low-lying swampy region near the Zambesi mouth - a region which, with its rank well-watered vegetation, its reedy swamps and wide stretches of tall elephant grass, its banana groves and plantations of maize, millet, and other cereals, and its abundant insect life, is evidently well suited to support immense numbers of these batrachians. Enough has been said to show that various species of *Megalixalus* and *Hyperolius* are conspicuously numerous, so as to represent a characteristic feature in the fauna. If other evidence of their abundance in suitable localities is needed, we may cite the case of *Hyperolius platyrhinus* Procter. Referring to a series of twenty-five specimens from Nyambita, Loveridge writes: "All these frogs were found upon the stems of twenty yards of *manyara* hedge, which they shared with half-a-dozen species of strange mantids and a snake (*Psammophis subtaeniatus*), which was coiled and sunning itself at a height of five feet from the ground."

In the case of the Canarian Tree frog (Hyla arborea var meridionalis) it has been calculated (Cott, 22 , p. 313), that an acre of banana plantation may support at least 1,500 individuals - or an adult population of approximately a million tree frogs to the square mile.

It therefore appears from the above facts that as predaceous enemies of insects - especially in the tropics - frogs and tree frogs take a prominent place.

ii. Intelligence and Power of Discrimination in Frogs.

In considering the part which frogs have played in the production of adaptive colouring, our next step must be to enquire to what extent, if at all, frogs are capable of learning to discriminate between palatable and harmful insects. Are these creatures absolutely indiscriminate feeders, the slaves of an inflexible feeding reaction? Or are they educable, capable of associating appearance with taste, and of learning by experience what is good to eat and what is not?

Experiments dealing with the feeding-habits of mammals and birds, devised to test the efficiency of warning and procryptic colours, are abundant, and in many cases, like those of Swynnerton, Hale Carpenter, Poulton, Pocock, and Marshall, are very detailed and extensive. But frogs have less frequently been the subject of similar experiments. In the matter of food discrimination and the formation of avoiding habits we have little information, and there is a good deal of contradiction in the conclusions drawn by various workers.

Some of the earlier work in this connection was done by Butler, who demonstrated that the larvae of Abraxas grossulariata were distasteful to frogs (11).

Poulton found that tree-frogs (Hyla arborea) when presented with flies and butterflies (which are "dusty, unsatisfactory things to eat") manifested a distinct preference for the former. "There is a most extraordinary difference in the behaviour of such a frog in the presence of a Housefly and of a Butterfly respectively, and in fact the latter is often disregarded." (93).

On the other hand, observations by Fisher and McAtee (67), Hodge (50), Kirkland (52), Garman (38), and others, to the effect that toads are known to eat aposematic insects such as wasps (Vespa polistes), squash bugs (Anasa tristis), potato beetles (Leptinotarsa decemlineata), etc., have been cited (67) as evidence that these creatures are more or less indifferent to warning colours and to the harmful qualities which they advertise. This view is not, however, justified by the facts, which have been discussed in some detail elsewhere (Cott, 20, pp. 528-532). These need not be referred to again here, beyond passing mention of the experimental work of Schaeffer (111), who showed (1) that frogs did not instinctively avoid unpalatable food; (2) that they learned after a few trials to discriminate between palatable and disagreeable insects; and (3) that the lesson was remembered for at least ten days.

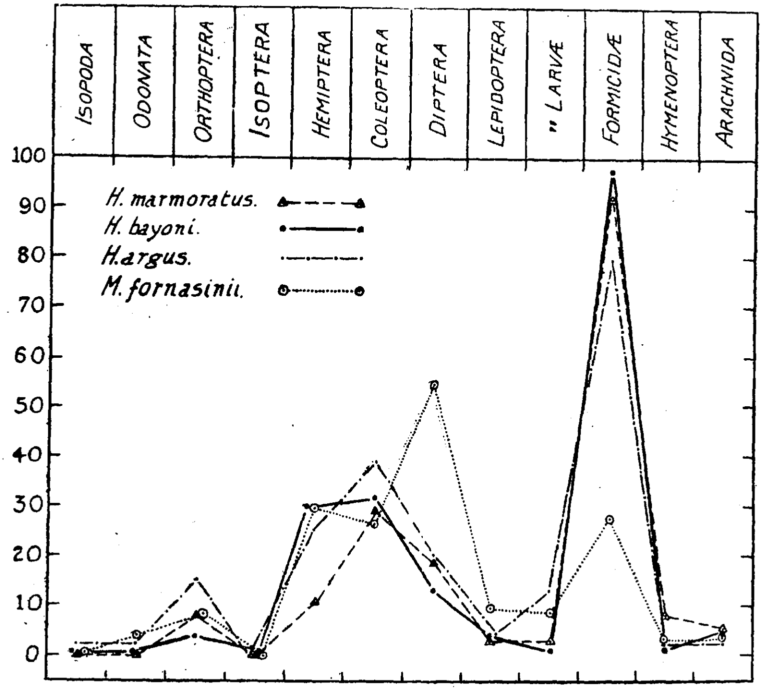
Further, and very conclusive, evidence on the question of discrimination and avoidance of unpalatable prey in the case of the toad will be found in Part V (pp.118-153).

iii. The Evidence afforded by Stomach Examinations.

If we turn from laboratory experiments to the laboratory of nature to study the reactions of frogs in relation to food, we find further evidence that the frog's behaviour - far from being limited by a fixed response to external stimuli - involves also the operation of such higher mental characteristics as memory, discrimination, and, apparently, of spontaneous action and a certain awareness of its environment. The creature knows, or learns to know, what is good to eat and what is not. Of the mental processes which lie behind these inspections, hesitations, rejections, and choosings we understand little. But I have no doubt that there is here much that cannot be explained in terms of clear-cut instincts and inflexible feeding reactions.

A comparison of data in the case of various species is instructive, and is graphically shown in text-fig. 9. These figures may be regarded, broadly, as indicating the

Text-figure 9.



The food-preferences of *Hyperolius marmoratus*, *H. bayoni*, *H. argus*, and *Megalixalus fornasinii* as indicated by the percentage of frogs containing various orders of food-animals.

TABLE XVIII.—Showing the number of Individual Tree-Frogs containing different Groups of Food-animals.

Insects, etc. from frogs' stomachs.	Number of stomachs containing various food-groups.				
	Hyperolius marmoratus.	*Hyperolius bayoni.*	**Hyperolius argus.*	*Megalixalus fornasinii.*	*Phrynobatrachus acridoides.*
Total no. of frogs with recognizable contents.	38	107	47	245	15
Isopoda	...	1	1	2	...
Odonata	...	1	1	10	...
Forficulidæ	1 } 3	1 } 4	2 } 7	5 } 20	...
Blattidæ	1	1	4	9	...
Gryllidæ	1	1	1	1	1
Acridiidæ	...	1	1	5	...
Termitidæ	...	1	...	...	...
Heteroptera (large)	...	2 } 32	3 } 12	6 } 72	...
Hemiptera (small)	...	9	...	7	2
Peregrinus	3 } 4	27	11	58	...
Aphididæ	1	...	...	8	...
Coleoptera (large)	...	3 } 34	2 } 18	13 } 65	...
Coleoptera (small)	11	32	17	55	5
Diptera (Muscid, etc.)	6 } 7	10 } 14	4 } 9	100 } 133	...
Diptera (Culicid, etc.)	2	4	6	53	4
Lepidoptera	1 } 2	4 } 5	2 } 8	23 } 43	...
Lepidoptera (larvæ)	1	1	6	21	...
Formicidæ	35 } 36	104 } 104	37 } 37	67 } 69	15 } 15
Hymenoptera	3	1	1	8	2
Arachnida	2	5	1	9	1

* The records for *H. argus* are incomplete, data for only 47 *individual* stomach-contents being kept, out of 254 frogs examined.

relative number of meals made from the various main groups of food-animals, i.e., Odonata, Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, Hymenoptera, and Araneida. In only four species were a sufficient number of individual contents recorded to furnish reliable data. However, from a study of these, certain interesting facts emerge:-
(1) In all four species the most popular food-insects consist of ants, beetles, bugs, and flies; (2) as regards the percentage of stomachs containing these orders, respectively, there is a surprisingly close agreement between the three species of Hyperolius, namely, H. marmoratus, H. bayoni, and H. argus; (3) a striking difference is observable in the case of Megalixalus fornasinii. Arranged in order of food-preferences, the results are as follows:-

H. marmoratus... Ants, 92 per cent.; beetles, 29; flies 18; bugs, 11.

H. bayoni....... Ants, 97 per cent.; beetles, 32; bugs, 30; flies, 13.

H. argus........ Ants, 79 per cent.; beetles, 38; bugs, 26; flies, 19.

M. fornasinii... Flies, 54 per cent.; bugs, 29; ants, 27; beetles, 26.

The difference between the food eaten by Megalixalus fornasinii and Hyperolius bayoni is strikingly brought out by the following figures, which are the more significant in view of the general similarity of habitat occupied by these tree frogs. So far as food-insects are concerned, there can be little difference in the environmental conditions - certainly not enough to account for these differences in diet.

Tree Frogs from the Borassus Palm forest region of the Lower Zambesi.

Food.	Megalixalus fornasinii (360).	Hyperolius bayoni (110).
Lepidoptera.....	4.8 per cent.	.2 per cent.
Diptera.........	26.3 " "	.4 " "
Hemiptera.......	46.3 " "	1.6 " "
Formicidae......	10.8 " "	96.2 " "

In a recent detailed investigation of the food of British Anura, I find strong evidence in support of the view that these animals discriminate in the choice of food. In a collection of frogs and toads taken both in the same habitat and under uniform conditions, the stomach contents of the two species were found to differ markedly:

Frogs and Toads from the heather moor, Lands End.

Food.	Rana temporaria (17).	Bufo bufo (45).
Mollusca.......	24.8 per cent.	.6 per cent.
Lepidoptera....	13.4 " "	2.4 " "
Diptera........	9.1 " "	.9 " "
Formicidae.....	.4 " "	41.4 " "

Further evidence of discrimination, and of avoidance of aposematic insects, will be found (20,p.476) in Table I , in text figure 3 , and in the tabulation of insects classified according to colour, pp.50-107. The following figures, which show the number of typically aposematic "AA" food animals included in the diet of certain East African and Canarian tree frogs, may be cited here as evidence of avoidance of unpalatable food.

Table XIX.

Species.	Total Prey.	Aposematic Prey.	Per cent.
Hyperolius marmoratus	2648	0	0.00
Hyperolius bayoni	3461	1	0.03
Hyperolius argus	3249	4	0.12
Megalixalus fornasinii	829	9	1.09
Megalixalus brachycnemis	31	0	0.00
Leptopelis johnstoni	6	0	0.00
Phrynobatrachus acridoides	564	0	0.00
Hyla arborea var. meridionalis	617	6	0.97

Finally, the following further evidence of differential food preference in the case of British Anura is based upon the identification of prey from the stomachs of about 600 frogs and toads.

4344 Hymenoptera recovered from Bufo bufo included only one Bumble Bee (Bombus) and three wasps (Vespa).

47 Hymenoptera recovered from Rana temporaria included a single bee (Andrena) and no wasps.

iv. Conclusion

It would be unwise, in the present state of our knowledge to attempt to draw any but tentative conclusions as to the part which frogs and tree-frogs have played in the evolution of warning colours and mimicry. We have not yet enough date as regards the intelligence of frogs, or their powers of discrimination and food-preferences, to speak with any certainty in the matter.

However, certain facts emerge which strongly point to the conclusion that frogs have not been impotent in bringing about these phenomena. In short, we have shown (1) that in view of the quantity of insect life destroyed by tree-frogs and other batrachians, and of the abundance in suitable localities of these forms, they may be regarded as serious enemies of insects in the tropics; (2) that the mental equipment and feeding-habits of frogs is such as to suggest their claim to a not unimportant share with birds and other insectivorous animals in the production of warning colours and mimicry; and (3) that an analysis of the insects eaten by tree-frogs, as revealed by stomach examinations of specimens freshly taken in their natural surroundings, lends indirect support to this conclusion.

PART V. THE EFFECTIVENESS OF PROTECTIVE ADAPTATIONS IN THE HIVE BEE, ILLUSTRATED BY EXPERIMENTS ON THE FEEDING REACTIONS, HABIT FORMATION, AND MEMORY OF THE COMMON TOAD.

We have seen above that apart from its more general ecological and evolutionary aspects, the subject of predation has a significant bearing on the theory of warning colours and mimicry. While supporters of these theories attach importance to the relative protection enjoyed by various aposematic animals, there is yet considerable difference of opinion as to the facts. The gathering of further reliable data on the feeding habits of animals in relation to the different protective devices by various types of prey is therefore greatly needed.

To this aspect of the adaptation problem there are four methods of approach, namely direct observations in the field on the feeding habits and behaviour of predatory animals; properly conducted feeding experiments with animals either in captivity or controlled under natural conditions; the study of the ecology and adaptations of the animals preyed upon; and the examination of stomach- and pellet- contents of wild animals.

Of these various methods, the first two are of considerable importance in that they furnish data relating to an animal's reactions in the presence of unpalatable prey, and to its power of association, and memory, which cannot be directly determined by the examination of stomach contents alone. The analysis of stomach-contents has been found by experience to furnish the most reliable statement of the food actually eaten in nature, but it can tell us little of the actual feeding behaviour, - of the predator's psychology, of its rejections and refusals.

The present Part is the outcome of a series of ex-:periments on the edibility of the hive bee. It represents an attempt (1) to throw some light on the feeding behaviour, power of association and discrimination, and memory in the common toad; and (2) to provide definite proof of the effectiveness of the protective adaptions of bees against predatory attack by these batrachians.

1. Material and Method

During the summer and autumn of 1933 I carried out experiments to determine whether hive bees are acceptable or distasteful to toads, and to discover - if they proved dis-:tasteful - how quickly the toads learned to recognise and to avoid these insects, and whether the lesson of avoidance, once learned, is remembered.

The toads used were adults of Bufo bufo bufo which had been captured near Glasgow in the previous April and May. The animals were quartered in a roomy vivarium under more or less natural conditions, being provided with an abundance of damp moss, ferns and other vegetation, and with boulders beneath which shelter and hiding places were available. They were fed upon a variety of insects, such as mealworms and cockroaches. Before the date of the first experiment they had become partially tame, having lost much of their natural shyness, and having grown accustomed to human society and to being handled.

For the purposes of identification each toad was marked with a numbered aluminium ring (similar to those used for marking wild birds) which was clipped round the arm. In the present communication the different individuals are referred to by their serial numbers - Nos. 1-34.

Toads undergoing test were placed, one at a time, upon the landing board of an active beehive. They were put down close to the entrance, and facing it, and were allowed the opportunity to feed, undisturbed, upon the outgoing and incoming workers. There they were left alone to feed freely without interruption until each voluntarily terminated the test by jumping down, sooner or later, from the platform. If during one of the trials a toad came to rest, and remained inert for a period of some fifteen minutes without showing signs of resuming activity, it was removed: but this happened exceptionally, and, as already stated, the usual procedure was to interfere with and influence the animals' movements as little as possible.

Two sets of trials were carried out. These are here referred to respectively as Experiment I and Experiment II. In Experiment I, thirty four toads (Nos. 1-34) - which had been kept without food for a week before the first trial -

were tested individually on the hives twice daily for seven consecutive days, their behaviour while undergoing test being carefully noted. No food other than bees was provided during the week of experimentation. After visiting the hive on the seventh day, the toads were allowed to feed freely on mealworms for twenty-four hours.

Eighteen of the above toads (Nos. 16-28, 30-34) which were used in Experiment II then rested for a fortnight, during which they were made to fast. In Experiment II the trials were repeated as before with these individuals for a further period of seven consecutive days. After the fourteenth visit to the hives, each toad was again allowed to feed freely on mealworms for twenty-four hours.

Records were kept of the behaviour of each toad during the several trials on the hives. Although a full account of each animal's reactions cannot be included in this paper, the essential data are given in condensed form in Tables XXI and XXII, where will be found records (i) of bees eaten, (ii) of internal and (iii) external stings received by the toads. While the first and the third of these are a matter of direct observation, the second could only be inferred by the toad's reactions. These, however, were frequently such as to leave little doubt as to their cause, and in the course of the experiments a combination of certain reactions by a toad after swallowing a bee came to be regarded as indicating a degree of discomfort that could only have its origin in an injection of poison. Such reactions included a sudden violent jump, jerky vertical bowing movements of the head, repeated withdrawal of the eyes into the head, exaggerated swallowing movements, often accompanied with mouth-wiping reactions with a forelimb, gaping mouth and protruding tongue. While it is therefore believed that records of stings based upon such movements represent undisputed injections of poison, it is not claimed conversely that all stings received could be observed and it is not unlikely that such occurrences took place, of which there is here no record.

Various precautions were taken to render the results as free as possible from errors due to chance, to climatic effects, and to the variable condition of the hives:-

(a) The experiments were attempted on a large scale, and it is believed that the considerable number of toads used, and the nature and number of trials undergone by each, were sufficient to render reliable statistical data. It has already been mentioned that the various trials on each day were duplicated. Thus 33 toads (excluding No. 29 which died) participating in Experiment I each carried out 14 trials, giving a total of 462 trials. Similarly the 18 toads used in both Experiments I and II each carried out 28 trials, giving a total of 504. In all a total of 714 trials (462 in Exp. I and 252 in Exp. II) ranging in duration from a few seconds to nearly an hour, and together extending over more than forty hours, were completed. In each of these trials a toad, hungry through fasting, had ample opportunity to accept or to refuse bees which were in all cases readily available as food.

(b) In order to counteract the effect of climate on the activity of the toads themselves, and on the swarms, the former were divided for experimental purposes into groups, which will be referred to as Series A,B,C,D, and E. With each of these Series the experiments were started on different dates and carried through independently, as shown in Table .

Table XX.

Toads	Experiment I	Experiment II
Series A (Nos.1-8)	10.6.33 - 16.6.33	
Series B (Nos.9-15)	16.6.33 - 22.6.33	
Series C (Nos.16-25)	5.9.33 - 11.9.33	26.9.33 - 2.10.33
Series D (Nos.26-30)	7.9.33 - 13.9.33	28.9.33 - 4.10.33
Series E (Nos.31-34)	11.9.33 - 17.9.33	2.10.33 - 8.10.33

(c) Care was taken to utilise a hive where conditions were favourable for the trial. When some thirty or more bees were crowding on the platform the hive was found to be unsuitable, for under such conditions the toads were liable to be intimidated or hustled off by the bees before having the necessary quiet opportunity to feed. Similarly inactive hives, with only an occasional bee entering or emerging and with no insects crawling about on the landing board were avoided, for here the toad might wander off the hive before encountering a bee. By selecting a particular hive (of seven available) and by choosing the time of day for the trial according to weather conditions, it was generally possible to maintain tolerably constant experimental conditions - the swarm selected being one that was active, with a fairly constant traffic of workers passing in and out of the entrance and with (say) from one to ten bees crawling about on the landing board. Under such circumstances, the bees were readily available for food and easy to catch, without being present in such numbers as to deter the toad, or drive it away, by their very abundance. When, as sometimes happened, workers collected to attack a toad during a trial it was usual to continue further trials on one of the other hives, at any rate until the disturbance caused by the toad's presence was over.

(d) It has already been mentioned that the toads were subjected to a period of starvation before the commencement of Experiment I, and during the interval of a fortnight between Experiments I and II. In the two weekly test periods, the toads were allowed no food other than the bees which were available during the actual trials at the hives. Finally, in order to show that the refusal of bees was due to unpalatibility of the food rather than to some other cause such as sickness, repletion or loss of appetite, each animal was allowed to eat its fill of mealworms during the twenty-four hours following the last visit to the hive, that is to say, at the termination of each Experiment.

2. Experimental Data.

Owing to limitations of space it is impracticable to give here a full account of the individual tests carried out, except in the case of a few toads, whose behaviour is recorded in the next section.

In Tables XXI and XXII, below, the essential observations relating to the whole series of trials have been condensed. It is only necessary here to add a few explanatory words.

The columns numbered from 1-7 refer to the seven consecutive days of experimentation. The different series of toads (see p.123) are represented by the horizontal divisions.

"1" indicates that a bee was snapped up and swallowed. In one case, where two bees were taken simultaneously (No.27) this is shown as "2". * indicates that the toad was apparently stung internally after swallowing a bee. Stings thus recorded are based upon such observed behaviour as was judged to indicate almost conclusively that the toad had received an injection (see p.121). + indicates that the toad received an external sting by a bee. o indicates that the toad was mobbed by workers and hustled off the hive, without apparently receiving a sting.

The time taken for the different trials (see Table XXIVa) depended, as already stated, upon the individual behaviour of each toad, which, when placed on the hive, was left to feed undisturbed, the trial normally terminating (after a period ranging from a few seconds to nearly an hour) by the voluntary departure of the toad, or by its being driven from the hive by the workers.

Table XXI. Experiment I. Summary of Daily Experimental Data relating to Series A,B,C,D and E.

Toad No.	1	2	3	4	5	6	7
1.	1,+1*	-	-	1	-	-	-
2.	1,1,1,1*	1,1,+	1*	1*	1	-	-
3.	1,++	1,o	1*	o	-	-	-
4.	++	1*o	-	-	1*	-	-
5.	1,1	1,1*	-	-	-	-	-
6.	1,+++o	-	-	+o	-	-	-
7.	-	1*	-	-	-	-	-
8.	1,1,o1++o	-	-	-	+o	-	-
9.	1	-	-	-	1*	-	-
10.	1*++o	-	-	+	-	-	-
11.	1,1*	-	-	-	-	-	-
12.	-	-	-	-	-	-	-
13.	+1*o	-	-	-	++o	-	-
14.	o	1	1	-	-	-	-
15.	1	-	++o	-	-	-	-
16.	-	1,1,1,1	-	-	-	-	-
17.	-	-	-	-	-	-	++(11+)
18.	1,1,1,1*	1*1,1*	1,1*1,1*	-	-	-	-
19.	++	-	-	-	-	-	-
20.	1*	-	-	o	-	-	-
21.	1,1*+	1,1*1,1,1,1	1*	oo	-	1*+o	o
22.	1	1,1,1,1	1	o	-	+	++
23.	1,1	1,1,1*	1,1	-	-	o	-
24.	++	1	-	1,o	-	-	-
25.	1,+	-	-	-	-	o	-
26.	1,1,1,1	1*1,1*1,1	1,1,1	1*	1,1,1	1	-
27.	1+	1,1,1	1	1,1*1,1	1,1*	1+	-
28.	1*1	1*1,1*	1,1	1,1*	-	-	-
29.	1,1	-	1	-	-	-	-
30.	1	-	-	-	-	-	-
31.	1,1	-	-	-	-	++	-
32.	1*	o	-	-	-	-	-
33.	1*	1*	-	-	-	-	-
34.	1*+o	++	-	-	-	-	-

Table XXII. Experiment II. Summary of Daily Experimental Data relating to Series C, D and E.

Toad No.	1	2	3	4	5	6	7
16	-	-	-	1*	-	-	-
17	-	-	-	-	-	-	-
18	1,1,1*	1,1	1	1,1	-	-	-
19	-	-	-	-	-	-	-
20	-	-	-	-	o	-	-
21	1,1,1,1*	1,1,1,1+++	-	-	+o	-	+o
22	-	o	1o	-	-	-	-
23	-	-	-	-	1*	-	-
24	-	-	-	-	-	-	-
25	-	-	1	-	-	-	-
26	1	1,1	-	1*1*1*	-	-	-
27	1,2	1*	-	-	1*+	-	-
28	1	-	1*	-	1*	1,1	-
30	-	-	-	-	-	-	-
31	-	-	-	-	-	-	-
32	-	-	-	-	-	-	-
33	-	-	-	-	-	-	-
34	-	-	-	-	-	-	-

Table XXIII. Showing the Number of Bees eaten by individual Toads of Series C, D and E on each of seven consecutive Days during Experiments I & II respectively.

	EXPERIMENT I.								EXPERIMENT II.							
Days:	1	2	3	4	5	6	7		22	23	24	25	26	27	28	28-29.
Toad No.	Bees eaten.							Meal-worms eaten.	Bees eaten.							Meal-worms eaten.
16.	0	4	0	0	0	0	0	21	0	0	0	1	0	0	0	8
17.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	6
18.	4	3	4	0	0	0	0	36	3	2	1	2	0	0	0	38
19.	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	3
20.	1	0	0	0	0	0	0	12	0	0	0	0	0	0	0	12
21.	2	6	1	0	0	1	0	24	4	4	0	0	0	0	0	19
22.	1	4	1	0	0	0	0	0	0	0	1	0	0	0	0	11
23.	2	3	2	0	0	0	0	19	0	0	0	0	1	0	0	16
24.	0	1	0	1	0	0	0	29	0	0	0	0	0	0	0	23
25.	1	0	0	0	0	0	0	18	0	0	1	0	0	0	0	10
26.	4	5	3	1	3	1	0	4	1	2	0	3	0	0	0	0
27.	1	3	1	4	2	1	0	11	3	1	0	0	1	0	0	16
28.	2	3	2	2	0	0	0	0	1	0	1	0	1	2	0	0
30.	1	0	0	0	0	0	0	6	0	0	0	0	0	0	0	10
31.	2	0	0	0	0	0	0	7	0	0	0	0	0	0	0	5
32.	1	0	0	0	0	0	0	12	0	0	0	0	0	0	0	11
33.	1	1	0	0	0	0	0	6	0	0	0	0	0	0	0	13
34.	1	0	0	0	0	0	0	9	0	0	0	0	0	0	0	12

Table XXIV. Showing (i) the daily total number of Toads which accepted Bees, and (ii) the daily total number of Bees eaten, by Series C, D, and E during the seven consecutive days of Experiments I and II respectively.

Days:	1	2	3	4	5	6	7	7-8
	(i) Number of toads eating (a) bees							(b)mealworms eaten.
Experiment I	14	10	7	4	2	3	0	16
Experiment II	5	4	4	3	3	1	0	16
	(ii) Number of (a) bees eaten							(b) mealworms eaten.
Experiment I	24	33	14	8	5	3	0	219
Experiment II	12	9	4	6	3	2	0	213

Table XXIVa. Showing the Daily Experimental Period spent on the Hive Platform by each Toad of Series B, C, D and E (Experiment I) and of Series C, D and E (Experiment II). (Records under this heading for Series A are incomplete and have been omitted).

Toad No.	Time in minutes.							Total
	1	2	3	4	5	6	7	
	Experiment I. Series B, C, D and E.							
9	4.0	14.5	16.5	5.5	9.5	1.5	1.5	53.0
10	2.0	14.5	2.5	6.0	2.0	1.0	1.5	29.5
11	6.0	8.0	4.5	11.5	5.0	3.5	2.0	40.5
12	1.5	2.5	9.0	9.0	11.0	7.5	3.5	44.0
13	1.0	8.0	40.0	26.0	2.5	1.0	2.0	80.5
14	2.0	5.5	6.0	5.0	22.0	2.5	3.5	46.5
15	7.5	5.0	.5	1.5	6.5	3.0	8.5	32.5
16	6.0	7.0	1.0	1.5	3.5	3.0	5.0	27.0
17	10.0	12.0	7.0	12.0	15.5	5.0	7.0	68.5
18	7.5	12.5	18.0	4.5	2.5	12.5	4.5	62.5
19	6.0	4.0	.5	.5	.5	.5	3.5	15.5
20	3.0	13.5	3.0	22.5	5.5	4.5	10.0	62.0
21	6.0	12.0	9.5	3.5	2.0	4.0	1.0	38.0
22	4.5	12.5	7.5	5.0	.5	7.5	2.0	39.5
23	3.5	12.0	3.5	1.5	2.0	1.5	2.5	26.5
24	.5	3.5	2.5	2.5	.5	2.5	.5	12.5
25	1.0	20.0	2.0	3.0	11.0	9.0	22.0	68.0
26	7.0	30.0	10.0	11.0	5.5	13.0	8.5	85.0
27	6.0	18.5	5.5	11.0	10.0	4.0	2.5	57.5
28	14.0	19.0	14.0	18.5	12.0	14.0	2.5	94.0
29	16.0	3.0	4.5	-	-	-	-	-
30	5.0	4.0	2.0	1.5	2.0	4.0	4.5	23.0
31	16.0	3.5	6.5	5.0	4.5	8.5	.5	44.5
32	5.5	3.5	3.0	5.5	7.0	1.0	.5	26.0
33	15.5	7.5	8.5	9.0	10.5	9.5	5.0	65.0
34	8.0	1.5	7.5	2.0	9.0	12.5	12.0	52.5
	Experiment II. Series C, D and E.							
16	4.0	8.0	9.5	55.5	31.0	18.0	19.0	145.0
17	6.0	10.0	10.0	10.0	7.0	15.0	10.0	58.0
18	6.5	15.5	8.0	41.0	8.0	4.0	57.0	140.0
19	3.0	9.0	9.0	5.0	11.5	1.0	6.5	45.0
20	19.5	27.5	3.0	4.5	4.0	3.0	5.5	67.0
21	7.5	9.0	3.5	19.0	.5	4.0	11.5	55.0
22	7.0	.5	2.5	11.0	1.0	11.0	7.0	44.5
23	3.0	7.5	18.5	23.0	46.0	27.0	27.0	152.0
24	3.0	5.0	2.0	4.5	8.0	3.0	4.0	29.5
25	6.0	8.0	10.5	22.0	17.0	6.5	8.0	78.0
26	15.0	27.0	2.5	20.0	.5	7.0	.5	72.5
27	4.0	15.5	3.0	9.5	1.5	5.5	4.5	43.5
28	18.0	8.0	11.5	7.0	15.0	24.0	3.5	87.0
30	3.0	3.0	2.0	2.5	3.0	5.5	3.0	22.0
31	1.0	1.0	2.0	3.0	1.0	4.0	4.5	16.5
32	7.5	3.5	2.5	2.5	3.0	5.5	2.5	27.0
33	1.0	1.5	2.0	3.0	10.0	15.5	10.0	43.0
34	4.0	5.0	1.5	7.0	10.0	7.0	3.0	37.5

3. Observations on the Behaviour of Individual Toads.

No. 18, ♀ , length 74 mm.

5 September. Placed upon the platform of hive i: the toad regards emerging and homing bees with apparent interest: hungry, and showing no signs of fear of the insects, she flicks at and misses three bees in succession as they crawl out of the hive. At the fourth attempt she is successful, snapping up and swallowing a bee with no apparent ill-effects. Three more bees are snapped up and swallowed in quick succession. Evidently stung by the last of these, she shows signs of discomfort - eye-closure and gulping movements. Taking no further notice of the bees, she crawls to the end of the platform, frequently closing the eyes, and jumping clear at 7 minutes. Replaced on hive i: she watches bees at the entrance closely for a few moments, and then deliberately turns round, walks away to the end of the platform, and jumps off.

6 September. On hive i: snaps up and swallows a bee: she is stung inside the mouth: gulping, with eyes closed, she walks backwards away from the entrance. At 3.5 minutes a second bee is eaten. At 7.5 minutes, snapping up and swallowing a third bee, she is stung again. After uneasy gulping and blinking movements which last one and a half minutes, she walks to and fro along the platform like a sentry, jumping off at 10 minutes. Replaced: she turns away and jumps at 12.5 minutes.

7 September. On hive vii: a bee is eaten. She now

backs away om being approached by another crawling bee. At 2 minutes a second bee is eaten, followed by convulsive movements of throat and general appearance of discomfort, the toad probably being stung. Having eaten a third bee shortly after this, she now appears to be afraid of the bees as they crawl around her, three times retreating backwards when approached by the insects. At 14.5 minutes a fourth bee is flicked up and swallowed, the toad being stung on the tongue. She now again retreats before advancing bees, jumping off the platform at 16.5 minutes. Replaced: she walks to end of platform, and jumps clear at 18 minutes.

8 September. On hive vii: she turns to watch two or three bees crawling about the platform, and then walks away from them without attempting to feed, jumping off the hive at 2 minutes. Replaced: bees within easy striking distance are ignored. She turns and walks away, presently returning to watch the movements of the insects, and after considerable crawling about and inspection she jumps off at 4.5. minutes.

9 September. On hive ii: she flinches at the sight of approaching bees, dropping the head, and then turning so as to face away from the bees passing through the entrance: jumps at 2 minutes. Replaced: the toad walks away immediately, and jumps clear at 2.5 minutes.

10 September. On hive i: She turns away at once, walking to the end of the platform, and jumping off at 10.5 minutes. Replaced: she watches several bees closely, then

turns away, jumping at 12.5 minutes.

11 September. On hive vii: Several bees come within easy reach and are left untouched. She turns to watch the insects, following their movements, but hesitates to approach, walking slowly away at 3.5 minutes and jumping at 4.5 minutes, after deliberately turning away from and crawling past bees within close reach. Replaced, she jumps almost immediately from the hive.

26 September. On hive i: toad appears eager for food. Three bees are flicked up and swallowed in quick succession with easy and hardly perceptible movements. Evidently stung by the third bee, she suddenly begins to oscillate the head and fore part of the body up and down with vigorous jerky movements. When these cease, she turns away, and jumps off at 5 minutes. Replaced: she gazes at the bees; then raising a fore leg she wipes her mouth with a sweep of the fore-arm, as if to clear away an unpleasant taste, and turns, quitting the hive at 6.5 minutes.

27 September. On hive vii: Toad taking a lively interest in moving bees: two are quickly snapped up and swallowed, after which she crouches motionless, with occasional gulping and uneasy movements, until 9.5 minutes, when she jumps off the hive. Replaced: she stares at bees; appears frightened when approached by a bee, and hops energetically away down the platform, climbing off the hive at 15.5 minutes. A change in the toad's manner of leaving the hive was apparent at this stage of

the experiment: instead of quitting the platform by leaping and landing heavily on the grass beneath, she had latterly been noticed moving about at the ends of the board as though seeking an easier way of descent, and now(and on most subsequent occasions) she showed considerable acrobatic skill in avoiding the fall by clambering down one of the front supporting legs of the hive.

28 September. On hive vi: watching bees at close range, as if with distrust, making no attempt to strike: she then quickly turns away and walks off to the end of the platform. At 1.15 minutes a passing bee is snapped up and swallowed. After this, she shows further signs of fear, retreating from the insects and leaving the hive at 3 minutes. Replaced: she goes away with hurried steps to the end almost immediately, crouching still and ignoring bees, and clambers off at 8 minutes.

29 September. On hive vii: one bee eaten. At 5 minutes she still shows interest in approaching bees, following them with active movements of the head, so as to keep the insects in the direct line of vision. At 7 minutes a second bee is eaten, after which she appears uneasy. At 13 minutes she walks slowly to the end of the platform. Returning at 20 minutes, she gazes once more at the bees moving at the hive entrance, but will not strike, and clambers off the hive at 37 minutes. Replaced: she will have nothing to do with the bees and leaves the hive at 41 minutes.

30 September. On hive vi: Disregrading the bees, she jumps off the hive at 5 minutes, having made no attempt to feed.

Replaced: she turns round from the hive entrance at once, and deliberately walks away, and off at 8 minutes.

1 October. On hive vi: crouches motionless, taking no notice of passing bees until one of the insects alights on her back, when she flinches, strikes a timorous attitude with her eyes closed, and turns away to the end of the board, climbing down at 3 minutes. Replaced: she turns and slowly walks away, disregarding all bees and jumping off at 4 minutes.

2 October. On hive vi: after crouching inert, and regarding bees until 6 minutes, she turns away and walks off with long strides to the end of the platform. At 7 minutes she returns, passing in front of the hive entrance to the opposite end of the landing board, ignoring all bees encountered en route, and waits, without taking further notice of the bees, until 56 minutes, when she climbs off the hive. Replaced: she pauses for a few seconds at the entrance, and then walks away and will have nothing to do with the bees, climbing off the hive at 57 minutes.

No. 19, ♀ , length 71 mm.

5 September. Placed upon hive vii: the toad stays still near the entrance, watching the bees: then the eyes are drawn into the skull and closed. At 2.5 minutes, being stung on the leg, she hurriedly leaves the hive. Replaced: she "feigns death" striking a sufficiently ridiculous attitude with the body flattened out, the head lowered and chin pressed against

the board, and the legs spread-eagled. Remaining thus, she is again stung at 6 minutes, whereupon she beats a hasty retreat from the hive.

6 September. On hive i: after staring at the bees in a dazed fashion for two and a half minutes, she hurries to the edge of the platform, jumping clear at 4 minutes. Replaced: she appears very frightened, working the legs convulsively and rushing off the hive with every appearance of panic.

7 September. On hive iii: she will not stay on the hive, running off immediately. Replaced: she is off again with the utmost haste.

8 September. On hive vii: As before, she rushes off the hive immediately on being placed on the platform. Replaced: she is off again in great panic.

9 September. On hive ii: Behaviour similar to that of yesterday.

10 September. Unlike the majority of the toads, which soon grew tame and displayed little uneasiness when handled, this specimen now struggles, goes into convulsive movements of the limbs, and runs and hops away from the hive for several feet at her top speed.

11 September. On hive vii: she flattens out, crouching motionless on the platform, jumping clear at 3.5 minutes. Replaced: she leaps off the hive at once.

26 September. On hive i: after crouching motionless, she jumps clear at 1 minute. Replaced: she remains inactive on the platform, jumping off at 3 minutes.

27 September. On hive vii: she stares in a dazed fashion at the crawling bees, moving away to the end of the platform at 4 minutes, and jumping at 6 minutes. Replaced: she struggles to be off, with vigorous sweeping movements of the limbs which prove ineffectual in carrying her off the hive. The convulsive movements then cease, and on regaining control of herself, she hops in great haste to the end of the board, where she halts. She then returns towards the entrance of the hive, but will have nothing to do with the bees, and jumps clear at 9 minutes.

28 September. On hive vii: after remaining still near the entrance for half a minute, she walks with sluggish strides to the end and jumps down at 1.5 minutes. Replaced: she squats motionless, remaining thus while many bees crawl over her head and body, and jumps clear at 9 minutes.

29 September. On hive vii: she struggles to escape on being picked up, arching the back and striking out vigorously with the hind limbs. When released on the hive platform, the escape reaction continues, the legs and arms striking out with convulsive ineffectual movements which more nearly resemble those of swimming than of running, the hind limbs striking out together. After a few seconds she crouches motionless, and then walks off along the board with hesitating,

stealthy strides, jumping off at 5 minutes. Replaced: she is off again immediately in a panic.

30 September. On hive vi: after struggling for a few moments, she crouches quietly, jumping down at 11 minutes. Replaced: off again almost immediately.

1 October. On hive vi: she at once starts along the platform with long rapid leaps. Pausing a moment near the end, she is startled when a bee alights on her back, causing her to give a mighty jump off the hive. Replaced: she crouches and stares at the bees in an apathetic manner, then turns away and jumps off at 1 minute.

2 October. On hive vi: raising her hind leg, with a characteristic gesture she wipes away an imaginary bee from her back, then crouches on the platform, with head bowed and chin resting on the wood: she jumps at 2.5 minutes. Replaced: squats, moving little, until leaping from the hive at 6.5 minutes.

No. 20, ♀, length 72 mm.

5 September. On hive vii: having pounced upon and eaten one bee, the toad is evidently stung. She gives a wild leap, takes a few paces backwards, opening the mouth and gulping, and then stays still - flattened out on the board, with the head depressed and the limbs projected outwards. Later she moves away into an angle formed by the side and face of the

hive, turning her back towards the enemy. On being approached by a bee she jumps aside, and leaps off the hive at 3 minutes. Replaced: she jumps off the hive immediately.

6 September. On hive i: at the sight of bees crawling near the hive-entrance, she quickly turns her back and will have nothing to do with them: off at 2 minutes. Replaced: she turns away, squatting at the edge of the board. At 6.5 minutes she returns to the hive-entrance, staring in a hesitating manner at the bees, and then, without attempting to stalk after or strike at the passing insects, she jumps clear at 13.5 minutes.

7 September. On hive vii: displays uneasiness on the approach of bees. When several of the insects begin to crawl over her body at 1 minute she retreats from the hive in a panic. Replaced: remains inert, jumping clear at 3 minutes.

8 September. On hive vii: she turns away from the bees grouped near the entrance, and wanders about the platform near one end, jumping down at 10 minutes. Replaced: she appears to be afraid of the bees, flinching or running away when approached. At 22.5 minutes she is mobbed by a number of bees and hurriedly leaves the hive.

9 September. On hive ii: after watching the insects for about a minute and a half, she is touched by a passing bee and at once hurries away to the platform edge. She then turns round and attempts to find a way of climbing up the front of the hive. Abandoning this, she jumps at 4.5

minutes. Replaced: she is off again within a minute.

10 September. On hive vii: she turns away and will have nothing to do with the bees: off at 4.5 minutes. Replaced: she again turns her back on the bees, and jumps off the hive almost immediately.

11 September. On hive vii: the weather being dull, she makes no attempt to flick up the bees which are sluggishly walking about on the platform and presenting numerous opportunities for easy capture. When one of the insects flies past close to her, she is seen to flinch. Many bees continue to crawl within easy reach, but all are ignored as food, the toad jumping down at 8 minutes. Replaced: she stares at and watches the insects' movements as though preparing to attack, - then suddenly turns aside, and jumps away at 10 minutes.

26 September. On hive vi: quickly turning back from the hive-entrance, at 6 minutes she returns to look at the bees: then, having made no attempt to snap at the insects, she once more turns aside, and jumps off at 11 minutes. Replaced: at 15 minutes she appears afraid, and backs away from some bees crawling along the platform towards her. Off at 19.5 minutes.

27 September. On hive vii: subjects the bees to a careful scrutiny, and then hurries to the end of the platform. After squatting motionless, she returns to stare at the insects moving about near the entrance. Off at 27 minutes. Replaced: she displays symptoms of panic, rushing off the platform at top speed.

28 September. On hive vi: pausing a moment to stare at the bees, she hurries with rapid strides to the end of the platform, jumping off at 2 minutes. Replaced: she rushes off as if panic stricken, and jumps clear at 3 minutes.

29 September. On hive vii: takes a prolonged look at the bees, turning away and jumping off the hive at 3 minutes. Replaced: she walks backwards to avoid an approaching bee, retires to the end of the platform, and gets down at 4.5 minutes.

30 September. On hive vi: after staring at bees moving near the entrance, she crawls away, being mobbed and hustled by some of the insects: off at 4 minutes. Replaced: she is off again at once with a wild jump.

1 October. On hive vi: she appears to be interested in the bees, following their movements but hesitating to attack. After prolonged staring she depresses and closes her eyes and at once moves off with long determined strides to the end of the platform, where she halts for a minute, jumping at 2.5 minutes. Replaced: she turns away from the bees after ten seconds, and begins to crawl away slowly to the end, jumping off in haste when a bee crawls onto her leg.

2 October. On hive vi: walking away from the entrance at 1.5 minutes, she jumps from the hive at 2.5 minutes. Replaced: she displays much agitation, moving convulsively and hurrying to the end of the board, where she waits for three minutes before jumping clear.

No. 21, ♀, length 70 mm.

5 September. On hive i: After staring at the bees moving about the landing board, the toad at first turns away. At 3.5 minutes a passing bee is snapped up and swallowed. Immediately afterwards a second bee is pounced upon and eaten, the toad apparently being stung on this occasion. After much gulping, she flinches nervously as a passing bee blunders into her head, and walks to the edge of the platform, with the mouth gaping and the eyes closed, being stung on the leg and jumping off the hive at 6 minutes. Replaced: she jumps off almost immediately.

6 September. On hive i: a passing bee is snapped up at once. Eating a second bee, the toad is stung. After gulping and making convulsive movements, signs of discomfort disappear, and she once more takes an interest in the moving insects. A third bee is eaten; whereupon the toad appears disgusted, walking backwards and then hurrying away to the end of the platform. At 2.5 minutes she returns to the entrance, stalks after a bee, and then when about to strike, she backs suddenly away. Later another bee is eaten, the toad then hurrying away to the end of the platform, but again turning back later to watch the insects. As if fascinated by their movements, she approaches and snaps up a fifth bee, jumping off the hive at 10.5 minutes. Replaced: another bee is eaten immediately. The toad then appears frightened of flying bees, but remains watching at the hive-entrance until

12 minutes, when she suddenly turns round, hurries to the edge of the platform and jumps down.

7 September. On hive vii: she snaps up and swallows the first bee coming within striking range, and is stung. At the sight of an approaching bee she then retreats, walking backwards with the mouth gaping. At 8.5 minutes she rushes off the hive in confusion. Replaced: on being surrounded by several bees, she runs away at top speed, jumping down at 9.5 minutes.

8 September. On hive vii: she advances in a hesitating manner towards a bee, stalking it as though about to strike; then, the bee turning and moving towards her, she appears to change her mind, halting and walking backwards. At 2.5 minutes she is hustled by a number of the insects and driven from the hive. Replaced: within a minute she is again hustled off the hive.

9 September. On hive i: she shows no apparent interest in the bees, walking away at 1.5 minutes. On hive ii: she walks hurriedly past the entrance to the further end of the platform, where she attempts to climb off the hive, and falls to the ground.

10 September. On hive vii: a passing bee is snapped up and swallowed. Evidently stung, the toad begins to make vigorous vertical jerking movements of the head. She leaves the hive at 4 minutes, being driven away by the bees and receiving at least one sting. Replaced: she will have no more

to do with the insects, and, though unmolested, she rushes off at once in a panic.

11 September. On hive vii: she is hustled by a number of bees and hurries off the hive at 1 minute. Replaced: she precipitates herself immediately from the platform.

26 September. On hive vi. The toad watches the bees with apparent interest: she strikes ineffectively at a passing insect. Three bees are then disposed of in succession. With a sweeping movement of the hind leg she wipes a bee from off her head. After eating a fourth bee she is apparently stung, crouching in evident discomfort with the mouth gaping. She then goes to the edge of the platform and remains looking outwards, paying no further attention to the bees and jumping down at 7.5 minutes. Replaced: she is off the hive in great haste, and struggles vigorously on being taken up in the hand.

27 September. On hive vii: a bee is snapped up and swallowed almost immediately. She then appears frightened when a bee settles on her leg, and hurries away to the end of the platform, nervously kicking away several bees that approach with vigorous movements of the hind limbs. At 2 minutes a passing bee is eaten. At 4 minutes a third bee is eaten. She still keenly follows the movements of the insects, as if about to strike, but hesitates to do so as the bees approach close to her. Eventually she snaps up and swallows a fourth bee, and is soon afterwards stung externally and driven off

the hive - at 9 minutes. Replaced: she rushes away in a panic, being severely stung, apparently three times, as she goes.

28 September. On hive vi: she will have nothing to do with the bees - walking to the end of the platform, and jumping down at 2 minutes. Replaced: remains inactive until a bee crawls onto her hind leg, when it is hurriedly wiped off, the toad jumping down at 3.5 minutes.

29 September. On hive vii: she watches the movements of the bees with apparent interest, but hesitates to strike. Then without attempting to feed, she turns away and walks to the end of the platform, crouching there motionless until 10 minutes, when she turns round so as to face the bees moving about the hive-entrance. After again turning away to the edge of the platform, she once more turns back to look at the bees. Once more she apparently decides to leave the insects alone, turning away to the end of the platform and there crouching motionless in a corner with her back to the bees. From this position she was removed at 19 minutes.

30 September. On hive vi: she would not remain on the hive an instant, jumping off as soon as released. Replaced: she is stung on the leg and hustled off the hive in confusion.

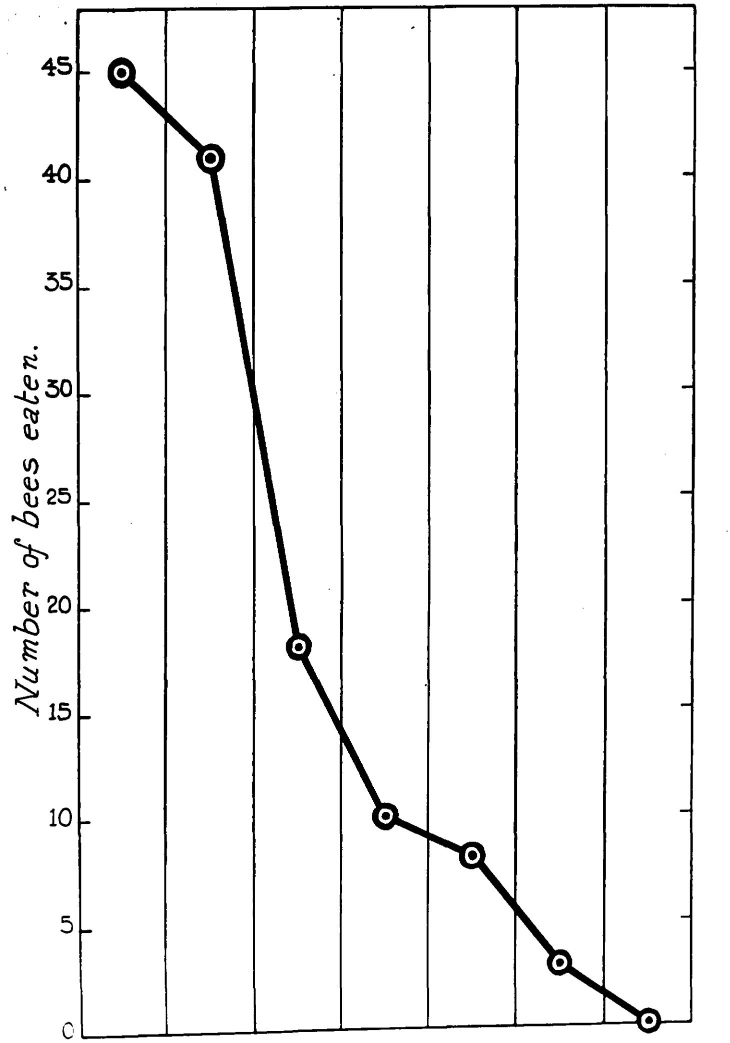
1 October. On hive vi: after looking at the bees, she backs away and turns sideways, then walks off to the edge of the platform. At 2.5 minutes she turns round so as to face

the bees, and after watching the insects for about half a minute, she turns and walks quickly to the end of the platform and jumps down. Replaced: she appears to get in a panic, struggling with convulsive movements which almost cause the animal to fall off the hive, and jumps clear at 4 minutes.

2 October. On hive vi: on being placed, as usual, near the entrance of the hive, she crouches motionless, ignoring the bees as they crawl within easy striking range. She then backs away from an advancing bee, and walks to the end of the platform at 3.5 minutes. At 10 minutes she turns, walks back to the entrance, and appears to be keen for food. While gazing at the insects, she is struck on the nose by an emerging bee, becomes nervous, and while hurrying away in apparent alarm she disturbs a number of the insects, being attacked, stung, and driven off the hive, at 11 minutes. Replaced: she appears to get in a panic, struggling, wiping imaginary bees off her back with vigorous sweeping leg movements, and then jumping down at 11.5 minutes.

4. Discussion.

Data relating to the number of bees eaten on each of seven consecutive days are graphically shown in Text figure 10. The drop from 41 bees eaten on the second day to 18 on the third is striking. It will also be noted that even the slowest



Text fig. 10.

toads had learned their lesson within seven days, and not one of the 33 individuals which completed the tests would touch the insects. This is all the more significant when it is remembered that the toads were hungry, having had no food other than bees for at least a fortnight. That these results were due to the distastefulness of the food rather than to a failure of appetite is shown by the test-feed of mealworms which was offered as a check after the experiment, when 29 (out of 33) toads eat a total of 444 mealworms.

The number of toads eating respectively from 1 to 6 bees daily tends to decrease progressively both for the number eaten and from day to day throughout the course of the experiment; while the number of toads refusing bees altogether shows a daily rise, from 8 (25 per cent.) to 33 (100 per cent.). These points are brought out in Table XXV.

Table XXV.

DAYS		1	2	3	4	5	6	7
Number of Toads Eating	6 bees	0	1	0	0	0	0	0
	5 bees	0	1	0	0	0	0	0
	4 bees	3	2	1	1	0	0	0
	3 bees	1	4	1	0	1	0	0
	2 bees	7	2	2	1	1	0	0
	1 bee	14	6	6	4	3	3	0
	0 bees	8	17	23	27	28	30	33

i. Rapidity of Habit Formation:

Experiment I.

The number of bees that required to be eaten before the habit of avoidance was established varied from one up to seventeen (No. 26). This wide difference in the rate of learning may be more apparent than real, for the ultimate rejection of bees depends upon previous individual experience, that is, upon receiving the stimulus which furnishes material for the association, and in many cases bees were swallowed without any evident ill-affects. Under such circumstances a toad would usually snap up another bee. This is seen in the case of both Nos. 2 and 18, each of which at the first trial eat four bees in succession, being only stung by the last mouthful, which put an end to feeding for the day.

These observations are in close agreement with the results obtained by Lloyd Morgan (75) in his experiments with young birds. This authority found that while young birds which received a sting quickly learned to avoid bees, if the bee was eaten without ill effects, others were not subsequently avoided. His experience with moorhen chicks illustrates this clearly. "Later, when they were a fortnight old, I threw them two bees, which were seized at once and without hesitation, and shaken violently. One of the birds was probably stung, for he shook his head, scratched the base of his bill, and went again and again to the water and drank. He was all right in about three-quarters of an hour, but for about that time scolded a good deal. The other ate his bee without any ill effects. A day or two after they were given a humble-bee, from which the sting had been removed, but the bird that had been stung would not go near the insect; the other seized and ate it. The next day two drone flies were given to them. The stung bird would not go near them; the other ate both." Lloyd Morgan concludes that "acceptance or avoidance is almost entirely due to the acquired results of individual experience."

Poulton has described somewhat similar behaviour on the part of a chamaeleon, which after attempting to eat, and being stung by, one bee, would thereafter have no more to do with the insects. "For many months after this I put bees into the cage at irregular intervals; but the chamaeleon's education in this direction was complete, the single experience was sufficient, and no other bee was touched." (94).

It was exceptional for a toad to continue feeding on any day after it had received an internal sting. Thus during this experiment, in which a total of 37 (apparent) internal stings were received by all the toads collectively, in 30 cases this put a stop to further feeding for the day. The record number of bees eaten by individual toads is 17 for No. 26 and 12 for No. 27, and in the light of the above remarks it is worth pointing out that these toads appeared to be especially fortunate in their experience with the bees, in receiving respectively only 3 and 2 internal stings, i.e., in each case approximately one sting for every six bees swallowed. On the other hand, it is significant that out of 33 toads used for the experiment no fewer that ten individuals learned to avoid the bees after a single trial acceptance: in nine of these cases, a single bee was eaten at the toad's first visit to the hive, and each on subsequent visits throughout the week, would have nothing more to do with the insects.

The following tables give an indication of the rate of learning as estimated (a) by the number of bees eaten and (b) by the number of internal stings received, by individual toads before the rejection of the insects was complete.

Table XXVI.

3	toads	eat	0	bees
10	"	"	1	bee
7	"	"	2	bees
3	"	"	3	"
2	"	"	4	"
1	toad	eats	6	"
1	"	"	7	"
2	toads	eat	9	"
1	toad	eats	10	"
1	"	"	11	"
1	"	"	12	"
1	"	"	17	"

Table XXVII

13	toads	received	0	internal	stings
12	"	"	1	"	sting
3	"	"	2	"	stings
2	"	"	3	"	"
2	"	"	4	"	"
1	toad	"	5	"	"

ii. Permanency of the Association:

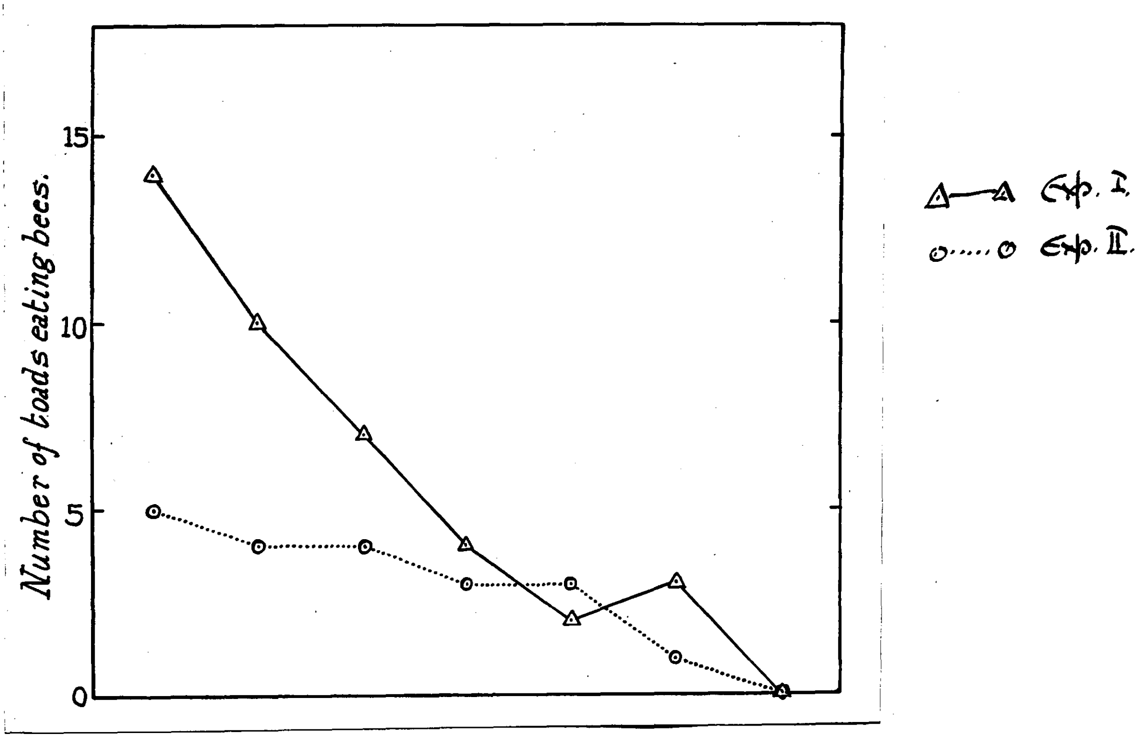
Experiment II.

The object of this experiment was to test the memory of toads which had previously learned to avoid bees. For this purpose the trials were repeated with 18 toads which had completed Experiment I a fortnight earlier, and which had in the interval been kept without food. With the exception of the fill-up on mealworms, which were offered immediately on the termination of Experiment I, these individuals had eaten no food other than bees for a month, and nothing at all for the past fourteen days: it must therefore be supposed that their appetite was considerably keener than at the commencement of Experiment I, which was undertaken after a fast (following regular feeding) of only one week.

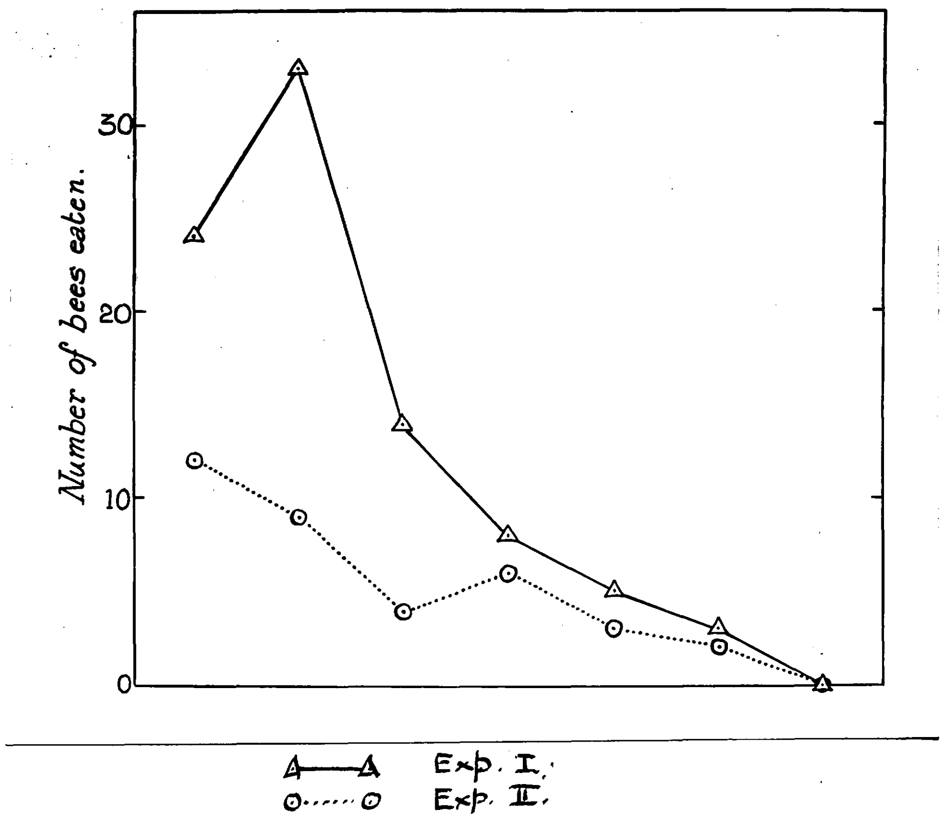
These facts render the experimental results obtained at the hives with Series C, D and E all the more striking. For on comparing the results of the present and earlier experiment, it will be seen (Tables XXVIII, XXIII) there is a general reduction both in the total number of toads which accepted bees, i.e., from 16 to 9; and in the number of bees actually eaten, i.e., from 87 to 36.

This is shown graphically in Text figures 10, 11.

Text-fig. 10.



Text fig. 11.



Further, on comparing the rate of learning by individual toads in the two experiments, it is significant that, with the exception of No. 25, which eat one bee during each set of trials (and of Nos. 17 and 19, which refused bees throughout both experiments), every individual toad shows an improvement in the diminished number of trial tastings necessary to re-establish complete avoidance (see Table XXVIII).

It will be noted from the figures below (1) that in no single case are more bees eaten by a particular toad in the second experiment; (2) that in several cases the improvement is very marked, as in No. 22 - from 6 to 1, No. 23 - from 7 to 1, No. 26 - from 17 to 6, No. 27 - from 12 to 5; (3) that

Table XXVIII.

Toad No.	Bees eaten.		Toad No.	Bees eaten.	
	Exp.I.	Exp.II		Exp.I.	Exp. II.
16	4	1	25	1	1
17	0	0	26	17	6
18	11	8	27	12	5
19	0	0	28	9	5
20	1	0	30	1	0
21	10	8	31	2	0
22	6	1	32	1	0
23	7	1	33	2	0
24	2	0	34	1	0

the total number of acceptances in the two experiments drops from 87 to 36 respectively, and (4) that the total number of toads refusing bees throughout the respective experiments rises from 2 to 9.

5. Conclusion.

These facts indicate sufficiently clearly (1) that bees are distasteful to, and well defended against, predatory attacks by toads; and (2) that even under starvation conditions and in spite of progressive hunger, these animals quickly learn to refuse the insects entirely, though afforded adequate opportunities to take them.

The foregoing experimental results strongly support conclusions based upon the examination of stomach contents - namely, that the mental equipment and feeding-reactions of Anura are such as to suggest their claim to a not unimportant share with birds and other insectivorous vertebrates in the production of warning colours and mimicry.

S U M M A R Y.

Part I.

(1) Concealing coloration depends for its success upon the creation of certain optical illusions, underlying which there are three fundamental principles: - (1) the resemblance in colour between an object and its background; (2) the obliteration of light-and-shade by counter lighting and shading; and (3) the breaking up of form by means of a superimposed disruptive pattern.

(2) Disruptive patterns are considered in relation to the habits and posture of the animals wearing them: a special aspect of disruptive coloration, described as coincident disruptive coloration, has for its essential feature the extension of the pattern across separate, but adjacent parts of the body. This greatly strengthens the disruptive effect of the pattern, for it unites the very parts of the body which are, in fact, separate entities.

(3) It is suggested that the colour-scheme and resting posture of M. fornasinii have a concealing and aggressive function which enables the species to exploit an abundant source of food available in the active, alert, and strongly-flying Odonata, muscid Diptera, and Lepidoptera - groups which are relatively inaccessible to, and little eaten by, the other tree-frogs whose habits were investigated.

(4) The leg-pattern has been investigated in Rana temporaria. Points of coincidence in pigment-bands across adjacent segments of the left leg occurred in 269 out of 300 frogs examined. Coincidence at one point occurred in 59 legs; at two points in 73; at three points in 69; at four points in 44; at five points in 15; at six points in 6; at seven points in two; and at eight points in one individual. In 55 legs the correspondence of pattern was between thigh and shin; in 48 between shin and foot; and in 166 there was coincidence right across the three segments of the leg.

Part II.

(5) A close parallelism has been shown to exist in the adaptive coloration of Insecta and Anura respectively: this resemblance has been traced through various types of concealing coloration (namely general protective resemblance, obliterative shading, disruptive coloration, coincident disruptive patterns, isolated distractive markings, flash colours, special protective resemblance), and has been specially treated in relation to the theory of warning colours.

(6) 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. Typical "warning" features, namely, conspicuous colours (black, black and white, black and yellow, black and red) and bold patterns (stripes, bars, ocelli) combined with aposematic habits, are found in many species, and, where these occur, they appear to be characteristically associated with highly poisonous secretions.

(7) Frogs are preyed upon by numerous enemies. They are hunted by small carnivorous mammals, by monitors, by fish, and by members of their own order; they are eaten by a wide range of birds, including crows, shrikes, kingfishers, owls, eagles, harriers, herons, bitterns, ibises, hammerheads, and spoonbills; and they are relentlessly persecuted by snakes, especially tree-snakes, which probably rank first in importance as enemies of tree-frogs in East Africa. In many cases the effectiveness of the secretion in protecting Anura from predatory enemies has been proved.

(8) Snakes and birds, the principal enemies of frogs, depend largely upon vision in hunting for prey. There is evidence that these enemies learn to discriminate between poisonous forms and those which are good to eat, and there is reason to believe that the warning mechanism, which advertises poisonous species in such compelling terms, is effective in assisting the education of enemies in the association of taste and colour.

Part III.

(9) The stomach-contents of 993 tree-frogs belonging to the following species are tabulated (the figures refer to the number of frogs examined and to the number of food-animals recovered):- *Hyperolius marmoratus*, 40 (2675); *H. bayoni*, 110 (3688); *H. argus*, 254 (3300); *Megalixalus fornasinii*, 360 (1119); *M. brachycnemis*, 11 (31); *Leptopelis johnstoni*, 8 (13); *Phrynobatrachus acridoides*, 15 (602); *Hyla arboria* var *meridianalis*, 195 (1210).

(10) 11,428 insects and other food-animals were obtained from the Zambesi frogs, - representing 11 orders and at least 153 species. Taken collectively, this material comprises the following groups of animals:- Hymenoptera, 87.16 per cent.; Hemiptera, 5.84; Diptera, 3.40; Coleoptera, 1.88; Lepidoptera, .70; Orthoptera, .46; Aranae, .34; Odonata, .15; Isopoda, .04; Ispotera, .02; Batrachia, .01.

(11) 1210 insects and other food-animals were obtained from the Canarian frogs, - representing 12 orders and at least 143 species. This material comprises the following groups of animals:- Hymenoptera, 58.18 per cent; Coleoptera, 16.54; Diptera, 6.12; Araneae, 5.78; Isopoda, 3.88; Hemiptera, 3.55; Lepidoptera, 3.06; Orthoptera, 1.07; Acari, .74; Chilopoda, .74; Neuroptera, .17; Amphipoda, .17.

(12) There is a close similarity in the food-habits of the three species of *Hyperolius* examined. Ants (*Pheidole megacephala*) in each case comprise more than 90 per cent. of the total; Hemiptera, Coleoptera, and Diptera, in varying proportions, make up the bulk of the remaining food. In contrast to the above, *Magalixalus fornasinii* is essentially a fly-catching frog - Diptera comprising the bulk of the food eaten.

(13) In *H. argus* certain differences have been observed (1) in the feeding-habits of the sexes, and (2) in the choice of habitat. These have been correlated respectively with the difference in the size of the sexes and with the marked sexual dichromatism in the species. The conspicuous colouring of the female, associated as it is with aposematic habits, may have a 'warning' significance.

(14) The frogs are considered in relation to their biological environment, with special reference to enemies and prey, and an attempt has been made to indicate certain 'food-chains' in which they form an essential link. There is evidence that these forms may be reckoned among the main predatory enemies of small insects in the tropics, and it is suggested that their depredations are not without economic value to man.

(15) The biological status of Hyla arborea in Gran Canaria and of Hyperolius argus in Portuguese East Africa is compared: a close parallelism, as regards both habitat and food preferences of these species is discussed. Both frogs, - belonging to unrelated species and inhabiting widely separate regions - in their respective environments, occupy the same ecological niche.

Part IV.

(16) An investigation of the food from the frogs' stomachs has been made (1) in order to test the efficiency of procryptic and warning colours, and mimicry, in defending insects from predatory attack; and (2) to indicate the part played by these batrachians as a factor in the production of adaptive coloration, in insects.

(17) Ants, which are usually regarded as well-defended insects, are widely used as food by frogs. Collected records of stomach examinations made by thirty-five investigators (embracing data relating to 153 species of Anura and to some thousands of individuals) shows that about 60 per cent. of the species examined include ants in their diet. This figure is only slightly exceeded in the case of one other kind of prey, namely, beetles.

(18) In the combined material from Zambesi and Canarian tree frogs, ants are represented by 10,632 out of 12,638 food-animals. The eight species examined each preys upon ants. These insects comprise the main food of the following species:- Hyperolius marmoratus, H. bayoni, H. argus, Phrynobatrachus acridoides, Megalixalus brachycnemis and Hyla arborea var. meridionalis, the percentage of ants in terms of total food-content being 98, 96, 93, 92, 77, and 57 respectively.

(19) In three species over 90 per cent. of the frogs containing recognizable food had been feeding upon ants. The figures for each species are as follows:- *P. acridoides*, 100 per cent; *H. bayoni* 97; *H. marmoratus* 92; *H. argus*, 79; *M. brachycnemis* 78; *L. johnstoni*, 33; *M. fornasinii*, 27.

(20) One is forced to conclude from these facts that the various phenomena of ant-resemblance, in so far as frogs are concerned, can have little, if any, adaptive significance.

(21) Hymenoptera (other than ants) comprise a significantly low percentage of the food, being represented in the Zambesi material by 20 specimens (i.e., .18 per cent. of food-animals) obtained from the stomachs of 18 frogs (i.e., less than 2.3 per cent. of those examined); and in the Canarian material by 9 specimens (i.e., .74 per cent. of food-animals) obtained from the stomachs of 7 frogs (i.e., 3.6 per cent. of those examined).

(22) The food-animals of the frogs have been classified according to colour-status, and the results are graphically shown for each of the following groups:- Orthoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera and Aranae. Of 10,968 specimens from Zambesi frogs sufficiently complete for analysis, not more than 48 insects are conspicuously coloured, and of these only 14 specimens (.13 per cent) belong to the typically aposematic group. Of 617 specimens from Canarian frogs, only 6 specimens (.97 per cent) belong to the typically aposematic group.

(23) These observations lend strong additional support to the classes of facts upon which the theory of warning colours rests: (1) that conspicuous pattern and colour in insects are typically associated with disagreeable or dangerous attributes which render their owner (relatively) unpalatable; (2) that insectivorous enemies learn by experience in nature to recognize and to avoid unpalatable prey; (3) that in leading to immediate recognition by enemies, and by checking the fatalities and injuries caused by experimental tasting, aposematic habits and colour are of vital benefit to their possessor.

(24) Tree-frogs are serious enemies of small insects in the tropics. They depend mainly upon sight in hunting and capturing prey. There are grounds for believing that they exercise discrimination in the choice of food, and that they learn to recognize and avoid unpalatable prey. There is strong presumptive evidence that aposematic colour and habit assist frogs in the recognition of distasteful species. The food-habits and mental equipment of tree-frogs is such as to suggest their claim to a not unimportant share with birds and lizards in the production, through natural selection, of procryptic and aposematic coloration in insects.

Part V.

(25) A series of experiments on the feeding reactions of the common toad are described and discussed. These experiments represent an attempt (1) to furnish reliable experimental proof of the effectiveness of the protective adaptations of hive bees in relation to toads; and (2) to throw some light on the feeding-reactions, powers of association, and memory in the common toad (*Bufo bufo*).

(26) In Experiment I. 33 toads (after a week's fast) were offered bees, but no other food, twice daily on seven consecutive days. The daily records of acceptance are as follows:- (a) Number of toads eating bees:- 25,16,10,6,5,3,0; (b) Number of bees eaten:- 45,41,18,10,8,3,0.

(27) No fewer than ten toads learned to avoid bees entirely after a single trial acceptance: in nine of these cases a single bee was eaten at the toads' first visit to the hive. By the seventh day the slowest individuals had learned the lesson of avoidance. On this day no bee was touched by any of the thirty-three toads which completed the tests.

(28) In Experiment II, which was carried out as a memory test, the trials were repeated as before after a fortnight's fast with eighteen toads which had previously learned the lesson of avoidance in Experiment I. Results showed a marked total reduction (1) in the number of toads which accepted bees - from 16 - 9; and (2) in the number of bees eaten - from 87 - 36; and an increase in the number of toads refusing bees throughout the respective experiments - from 2 - 9.

(29) A comparison of the rate of learning by <u>individuals</u> in the two experiments respectively, - as indicated by the number of trial acceptances necessary to establish complete avoidance - reveals (1) that in 15 out of 18 cases there is a definite improvement; (2) that in several cases the improvement is marked, as from 6 to 1, from 7 to 1, from 17 to 6, and from 12 to 5; and (3) that <u>in no single case is there an increase in the number of bees eaten</u>.

(30) These facts indicate sufficiently clearly (1) that bees are distasteful to and well defended against predatory attack by toads; and (2) that even under starvation conditions and in spite of progressive hunger, these animals quickly learn to refuse the insects entirely, though afforded adequate opportunities to take them.

(31) The foregoing experimental results strongly support the conclusions based upon the examination of stomach-contents, - namely that the food-habits and mental equipment of Anura are such as to suggest that these animals have played a part with birds and other insectivorous vertebrates in the evolution, through natural selection, of warning colours and mimicry.

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APPENDIX I.

The Zoological Society's Expedition to the Zambesi, 1927.

Batrachia and Reptilia.

The combined collections of living and preserved material from South and Portuguese East Africa are represented by 1,892 specimens belonging to 101 species. The numbers are distributed as follows:- Anura 1243; Chelonia 72; Crocodilia 1; Lacertilia 441; Ophidia 135.

Table XXIX contains the list of species, with locality records. Those which represent additions to the menagerie are marked with an asterisk (*). ** indicates species new to the Society's Collection. Descriptions of new species of frogs and lizards will be found respectively under Parker (90) and Cott (21).

TABLE ~~II.~~ XXIX.

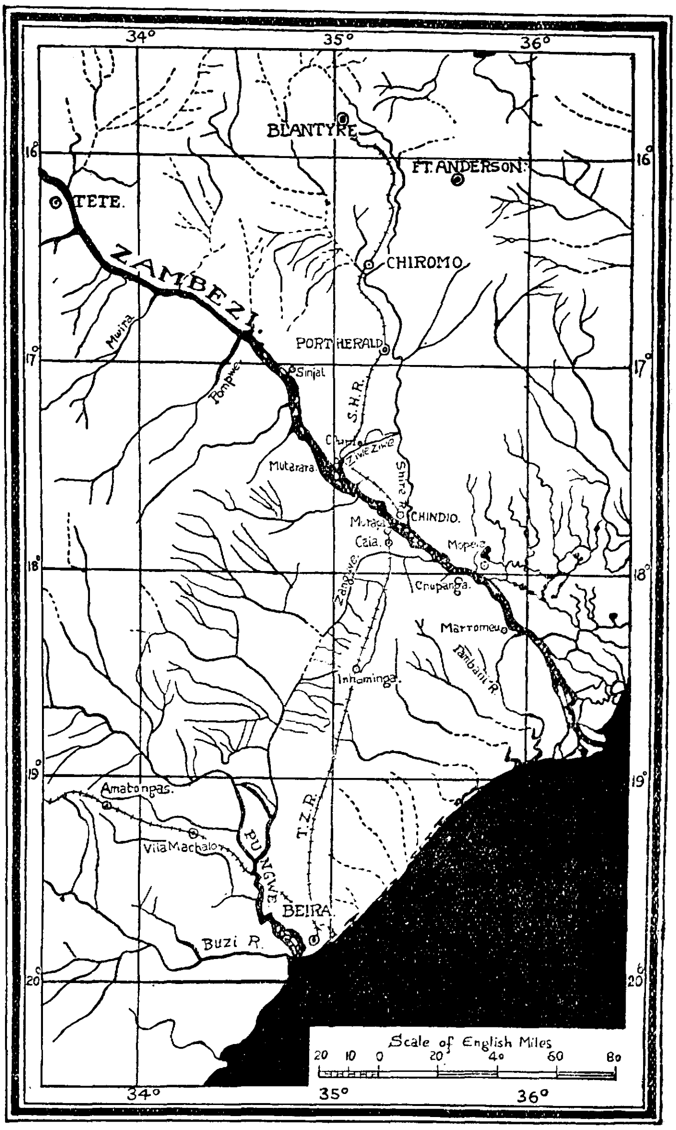
	Sinjal.	M'Gaza.	Charre.	Mutarara.	Caia.	Fambani.	Beira.	Amatongas.	Mortimer, C.P.
BATRACHIA.									
ANURA.									
RANIDÆ.									
*1. *Rana adspersa* (Tschudi)	...	...	...	+	+	+	...	...	..
2. *Rana delalandii* (Tschudi)	...	...	...	+	...	...	...	...	+
3. *Rana galamensis* Dum. & Bib.	...	...	...	...	...	+	...	...	...
4. *Rana angolensis* Bocage	...	...	...	...	...	...	...	+	...
5. *Rana nutti* Boulenger	...	...	...	...	...	...	...	+	...
6. *Rana ansorgii* Boulenger	...	...	...	...	...	...	...	+	...
7. *Rana oxyrhynchus* Smith	...	...	+	...	+	+	...	+	...
*8. *Rana mascareniensis* Dum. & Bib.	...	...	+	...	+	...	...	...	...
9. *Rana fuscigula* Dum. & Bib.	...	...	...	...	...	...	...	...	+
10. *Abrana cotti*, sp. n.	...	...	+	...	...	...	...	...	...
11. *Arthroleptis stenodactylus* Pfeffer	...	...	...	...	..	...	...	+	...
12. *Phrynobatrachus acridoides* (Cope)	...	...	+	...	...	+	...	+	...
13. *Phrynobatrachus natalensis* (Smith)	...	...	...	...	...	...	...	+	...
POLYPEDATIDÆ.									
14. *Chiromantis xerampelina* Peters	...	...	+	...	...	...	...	...	...
15. *Hylambates maculatus* Dum.	...	...	...	...	+	...	...	+	...
*16. *Leptopelis johnstoni* (Boulenger)	...	...	+	...	+	+	...	...	...
17. *Kassina senegalensis* (Dum. & Bib.)	...	..	...	...	...	+	...	...	...
18. *Megalixalus brachycnemis* Boulenger	...	...	...	...	+	+	...	...	...
*19. *Megalixalus fornasinii* (Bianconi)	...	...	+	...	+	+	...	...	...
*20. *Megalixalus loveridgii* Procter	...	...	+	...	...	...	...	...	...
21. *Hyperolius concolor* (Hallowell)	...	...	+	...	+	...	...	...	...
*22. *Hyperolius marmoratus* Rapp.	...	...	+	...	+	+	...	...	...
23. *Hyperolius bayoni* (Boulenger)	...	...	+	...	...	+	...	...	...
*24. *Hyperolius argus* Peters	...	...	...	...	+	+	...	...	...
25. *Hyperolius mossambicus*, sp. n.	...	...	...	...	...	+	...	...	...
26. *Hyperolius microps* Günther	..	...	...	...	...	+	...	...	...
BUFONIDÆ.									
*27. *Bufo regularis regularis* Reuss	...	...	+	...	+	+	...	+	+
PIPIDÆ.									
28. *Xenopus lævis* (Daudin)	...	...	...	...	...	...	...	+	...
29. *Xenopus mülleri* (Peters)	...	...	...	...	...	+	...	+	...
BREVICIPITIDÆ.									
*30. *Hemisus marmoratum* (Peters)	...	...	+	...	...	+	...	...	...
31. *Breviceps mossambicus* Peters	...	...	+	...	...	...	...	...	...
*32. *Phrynomantis bifasciata* Smith	...	...	...	...	+	...	...	...	...
REPTILIA.									
CHELONIA.									
TESTUDINIDÆ.									
*33. *Cinixys belliana* Gray	...	...	+	...	+	...	...	+	...
*34. *Hmopus areolatus* Thunb.	...	...	...	...	...	...	...	...	+

TABLE II. (*continued*).

	Sinjal.	M'Gaza.	Charre.	Mutarara.	Caia.	Fambani.	Beira.	Amatongas.	Mortimer, C.P.
TESTUDINIDÆ (*con.*).									
*35. *Testudo pardalis* Bell	...	...	...	...	...	...	...	...	+
*36. *Testudo angulata* Schw.	...	...	...	...	...	...	...	...	+
PELOMEDUSIDÆ.									
*37. *Sternothærus nigricans* (Donnd.)	...	...	...	...	+	...	...	...	...
*38. *Sternothærus derbianus* (Gray)	...	...	+	...	...	...	+	...	...
*39. *Pelomedusa galeata* (Schoepff.)	...	...	...	...	...	...	...	...	+
CROCODILIA.									
CROCODILIDÆ.									
*40. *Crocodilus niloticus* Laur.	...	...	...	...	+	...	...	...	...
LACERTILIA.									
GECKONIDÆ.									
*41. *Hemidactylus mabouia* Mor.	...	+	+	...	+	+	+	+	...
42. *Lygodactylus capensis capensis* (Smith)	...	...	..	...	+	+	+	+	...
**43. *Homopholis wahlbergii* (Smith)	...	...	...	...	...	...	...	+	...
*44. *Pachydactylus bibronii* Smith	...	...	+	...	...	...	...	...	+
45. *Pachydactylus mariquensis* Smith	..	..	...	...	...	...	...	...	+
AGAMIDÆ.									
*46. *Agama hispida armata* (Peters)	...	...	+	...	+	...	...	+	...
47. *Agama mossambica* Peters	...	...	+	...	+	+	...	+	...
**48. *Agama atricollis* Smith	...	...	...	...	...	...	...	+	...
**49. *Agama aculeata* Merr.	...	...	...	...	...	...	...	...	+
50. *Agama atra atra* Daudin	...	...	...	...	...	...	...	...	+
ZONURIDÆ.									
51. *Zonurus parkeri*, sp. n.	...	...	...	...	...	...	...	+	...
*52. *Zonurus cordylus* (Linn.)	...	...	...	...	...	...	...	...	+
**53. *Zonurus polyzonus* (Smith)	...	...	...	...	...	...	...	...	+
VARANIDÆ.									
*54. *Varanus niloticus* (Linn.)	...	...	+	...	+	...	+	...	...
AMPHISBÆNIDÆ.									
55. *Monopeltis mossambica*, sp. n.	...	...	...	...	+	...	...	...	...
56. *Chirindia bushbyi*, sp. n.	...	...	...	...	...	...	...	+	...
57. *Amphisbæna quadrifrons* Peters	...	...	+	...	...	...	...	...	...
LACERTIDÆ.									
58. *Nucras intertexta cameranoi* (Bedriaga)	...	...	+	...	...	...	...	+	...
59. *Ichnotropis squamulosa* Peters	...	...	+	...	...	...	...	...	...
**60. *Eremias namaquensis* Smith	...	...	...	...	...	...	...	...	+
**61. *Eremias lineo-ocellata* Dum. & Bib.	...	...	...	...	...	...	...	...	+
62. *Holaspis guentheri* Gray	...	...	...	...	...	...	...	+	...
GERRHOSAURIDÆ.									
*63. *Gerrhosaurus flavigularis flavigularis* Wiegm.	...	...	+	...	+	...	...	+	...
*64. *Gerrhosaurus major* Dum.	...	...	...	...	+	...	...	+	...

TABLE XXIX. (*continued*).

	Sinjal.	M'Gaza.	Charre.	Mutarara.	Caia.	Fambani.	Beira.	Amatongas.	Mortimer, C.P.
SCINCIDÆ.									
65. ***Mabuia quinquetæniata*** **(Licht.)**	+	...	...	...	...	...	...	...	...
66. ***Mabuia lacertiformis* **(Peters)**	...	...	...	...	+	...	+	...	...
67. ***Mabuia varia*** **(Peters)**	...	...	+	...	...	...	...	+	...
*68. ***Mabuia striata*** **(Peters)**	...	...	+	...	+	+	+	+	...
*69. ***Lygosoma sundevallii*** **(Smith)**	...	...	+	+	+	+	...	+	...
70. ***Ablepharus wahlbergii*** **(Smith)**	...	...	...	...	...	+	...	+	...
CHAMÆLEONTIDÆ.									
*71. ***Chamæleon dilepis dilepis*** **Leach**	...	...	+	...	+	...	...	...	...
*72. ***Chamæleon pumilus*** **Daud.**	...	...	...	...	...	...	...	...	+
OPHIDIA.									
TYPHLOPIDÆ.									
73. *Typhlops mucruso* (Peters)	...	...	+	...	...	...	...	...	...
LEPTOTYPHLOPIDÆ.									
74. *Leptotyphlops distanti* (Boulenger)	...	...	+	...	...	...	...	...	...
PYTHONIDÆ.									
*75. *Python sebæ* (Gmelin)	...	+	...	...	...	...	...	...	...
COLUBRIDÆ.									
*76. *Natrix olivaceus* (Peters)	...	...	...	...	...	+	...	...	...
77. *Ablabophis whytii* (Boulenger)	...	...	+	...	...	...	...	...	...
*78. *Boædon lineatus* Dum. & Bib.	...	+	+	...	+	+	...	...	+
*79. *Lycophidion capense* Smith	...	...	+	...	+	+	...	...	...
80. *Chlorophis hoplogaster* (Günther)	...	...	...	...	...	+	...	...	...
*81. *Chlorophis neglectus* (Peters)	...	...	+	...	+	+	...	...	...
*82. *Chlorophis irregularis* (Leach)	...	...	+	...	...	+	...	...	...
*83. *Philothamnus semivariegatus* (Smith)	...	+	+	...	...	+	...	...	...
84. *Coronella semiornata* var. *mossambicæ*, var. n.	...	...	+	...	...	+	...	...	...
*85. *Dasypeltis scaber* (Linn.)	...	...	+	...	...	...	...	...	...
86. *Tarbophis semiannulatus* (Smith)	...	...	...	...	+	...	...	...	...
*87. *Crotaphopeltis hotambœia hotambœia* (Laur.)	...	+	+	+	+	+	...	...	...
*88. *Psammophis subtæniatus* Peters	...	+	...	...	+	...	...	...	...
*89. *Psammophis sibilans* (Linn.)	...	+	+	...	...	...	...	...	...
*90. *Thelotornis kirtlandii* (Hallowell)	...	+	...	...	...	+	...	...	...
*91. *Dispholidus typus* (Smith)	...	...	...	...	...	+	...	...	+
*92. *Calamelaps warreni* Boulenger	...	...	...	...	+	...	...	...	...
93. *Naia haie* (Linn.)	...	...	+	...	...	...	...	...	...
*94. *Naia melanoleuca* Hallowell	...	...	+	...	...	...	...	...	...
*95. *Naia nigricollis* Reinhardt	...	...	+	...	...	+	...	...	...
*96. *Sepedon hæmachates* (Lacép.)	...	...	+	...	...	...	...	...	...
*97. *Dendraspis angusticeps* (Smith)	...	...	+	...	...	...	...	...	...
VIPERIDÆ.									
98. *Causus defilippi* (Jan)	...	...	+	...	...	+	...	...	...
99. *Vipera superciliaris* Peters	...	...	+	...	+	+	...	...	...
*100. *Bitis arietans* (Merrem)	...	+	+	...	+	+	...	+	...
101. *Atractaspis rostrata* Günther	...	...	+	...	...	...	...	...	...



Map of Zambesi Valley from Tete to Chinde, showing the localities from which specimens were obtained.

Pl. I.

FROGS FROM PORTUGUESE EAST AFRICA.

EXPLANATION OF THE PLATE.

Fig. 1. *Hyperolius mossambicus*, sp. n.

Figs. 2 & 3. *Hyperolius argus* Peters, adult males.

4, 5, & 6. *Hyperolius argus* Peters, immature females showing stages in the development of the adult coloration.

7 & 8. *Hyperolius argus* Peters, adult females.

Pl. II.

H. B. Cott. Photo.

Rana temporaria, Linn. Sussex.

H.B.Cott, Photo.

Ceratophrys cornuta.

Pl. III.

Pl. IV.

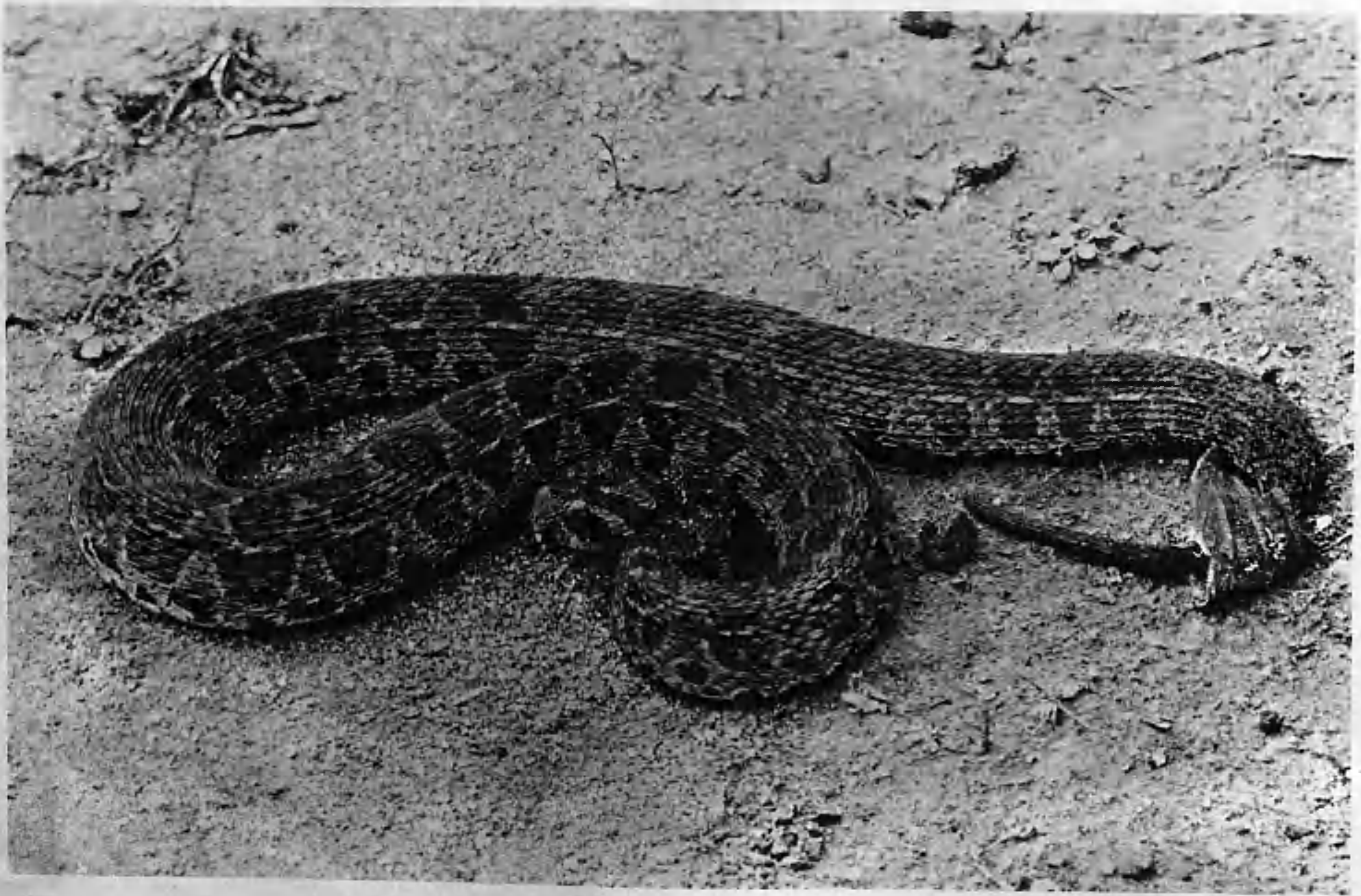
Photo. H.B.Cott.

Hyla langsdorffii. Santa Catherina.
B.M. No. 88.11.30.5.

Pl. V.

White cock photographed in front of white background, showing effect of lighting.

Vipera superciliaris, Peters.



John Bale Sons & Danielsson, L[td] London

VIPERA SUPERCILIARIS PETERS. FROM LIFE. CHARRE.

Pl. VI.

Pl. VII.

Photo. H.B.Cott.

Scolopax rusticola Linn.

Megalixalus fornasinii Bian.

Characteristic crouching attitude, illustrating disruptive type of concealing coloration.

Pl. IX.

H. B. Cott, Photo.

Kassina senegalensis D. & B.

Lower Zambesi.

(Showing coincident disruptive bands, – one of which extends across the three segments of the folded leg.)

Pl. X.

1.

H. B. Cott, Photos.

<u>Bufo valliceps</u>. Nicaragua.

B. M. No. 1908. 5. 29. 119.

2.

<u>Eupemphix nattereri</u>. Paraguay.

B. M. No. 85. 9. 1. 18.

Pl. XI.

1.

H. B. Cott, Photos.

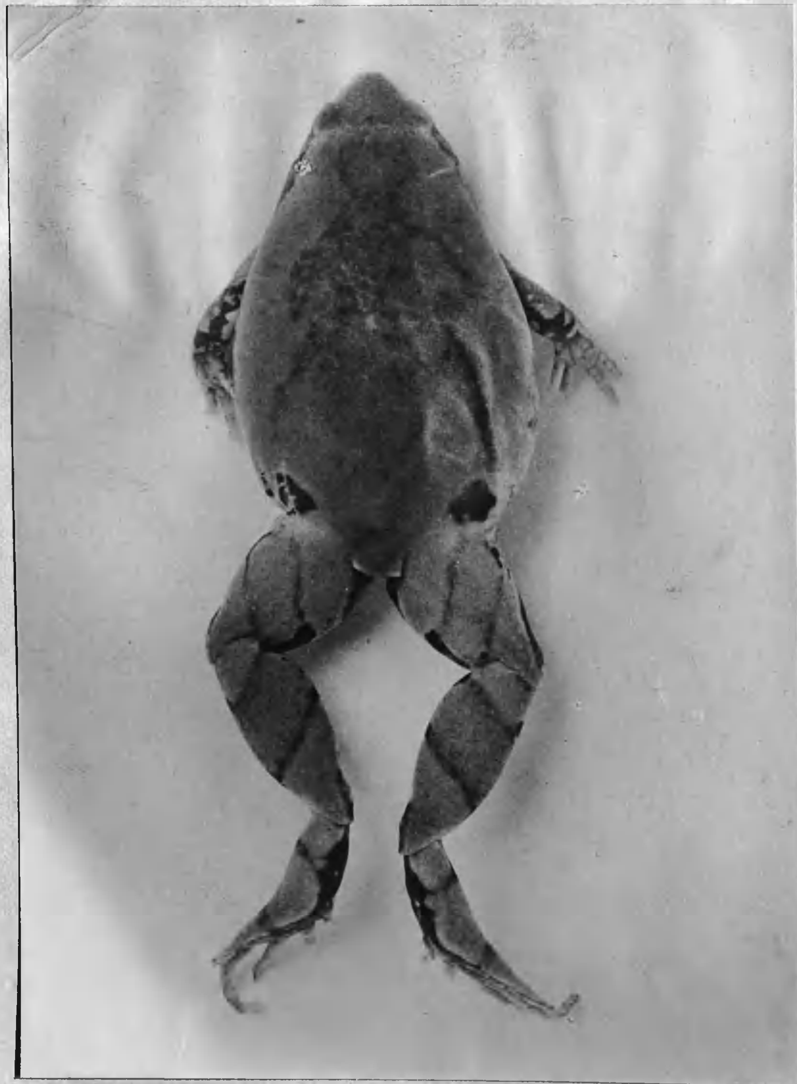
Bufo typhonius, Linn. Colombia.
B. M. No. 1916·4·7·29

2.

Bufo typhonius Linn
B. M. No. 9·8·4·28·133

Pl. XI.

1.



H. B. Cott, Photos.

Gastrophryne elegans.
B.M. No. 56.3.17.27

2.

Kalophrynus interlineatus.

1.

2.

H.B.Cott. Photos.

Edalorhina buckleyi. Canelos.
B.M. No. 80.12.5.194

Atelopus flavescens. Brazils.

Pl. XIII.

Pl. XIV.

H. B. Cott. Photo.

Bufo typhonius Linn. Pará.

Pl. XV.

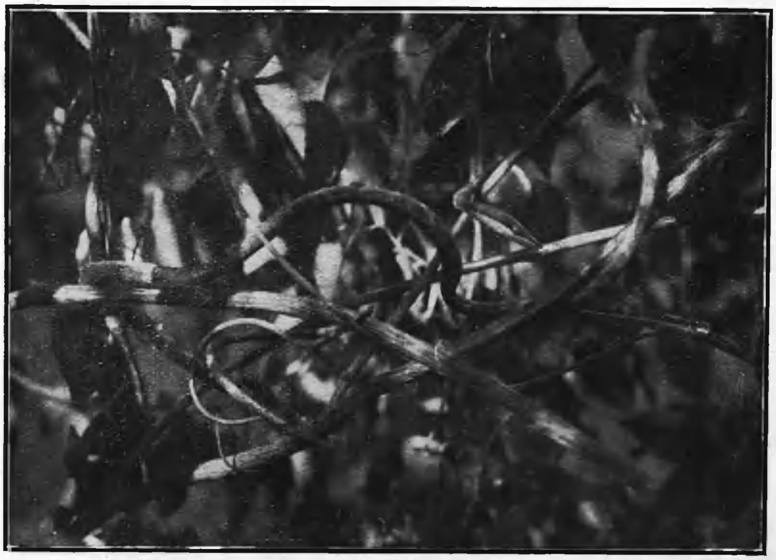
H. B. Cott. Photo.

"Blood Vein" (*Timandra amata*)

Yateley.

Pl. XVI.

1.



[Photo., H. B. Cott.

A.—OXYBELIS ACUMINATUS.

Lower Amazon.

2.

H.B.Cott, Photo.

Chiromantis xerampelina Peters

Lower Zambesi.

Pl. XVII.

H. B. Cott, Photo

Unidentified Tree Frog.
Lower Amazon.

Pl. XVIII.

H. B. COTT PHOT. *Natural Size*

Hawkmoth (*Xanthopan m. morgani*, ♀) at rest on bark of *Casuarina*; Beira, July, 1927

Pl. XIX.

Acrida sulphuripennis. Caia P.E. Africa.

Pl. XX

H.B.Cott. Photo.

Hyperolius marmoratus Rapp.

Portuguese East Africa.

Pl. XXI.

1.

Plate II. B.—BUFO MARINUS. [Photo., H. B. Cott.

Lower Amazon

2

Phot.

Phrynomantis bifasciata Smith.