PARC NATIONAL DE L'UPEMBA. — MISSION G. F. DE WITTE

en collaboration avec

W. ADAM, A. JANSSENS, L. VAN MEEL et R. VERHEYEN (1946-1949)

Fascicule 64

THE FOOD OF AMPHIBIANS

BY

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INTRODUCTION

The material on which this study is based was collected in the Parc National de l'Upemba, Province of Katanga, Congo. The park, situated between 8°15′ and 9°50′ S and 26° to 27°10′ E, lies south of the rain forest belt and is covered by a mixture of grass savanna, savanna woodland, and marshes (VERHEYEN, 1953). The topographic relief in the Upemba is extensive, the elevations ranging from 585 to 1,830 m above sea level. Rainfall is markedly seasonal (Fig. 1); the five months May to September have less than 25 mm of precipitation and the other months 100 to 200 mm.

The amphibian fauna consists of 51 species (LAURENT, 1957; SCHMIDT and INGER, 1959) : *Xenopus* (1 species), *Bufo* (6), *Rana* (17), *Arthroleptis* (2), *Cacosternum* (1), *Phrynobatrachus* (6), *Leptopelis* (2), *Kassina* (2), *Afrixalus* (2), *Hyperolius* (10), *Hemisus* (1), *Phrynomerus* (1). These include aquatic, terrestrial, arboreal, and fossorial species, and adults varying in size from 15 to 100 mm.

The basic question in this study is : What does the diet of each species consist of ? Taxonomic analysis of the diet, the first step in answering the question, may be qualitative and quantitative. Given the large number of specimens available for the species analyzed (SCHMIDT and INGER, ibid.), the quantitative aspect should be dealt with. We have posed three taxonomic questions for each species : What taxonomic groups are included in the diet ? Are the relative proportions of these groups equal ? If not, which categories form the largest proportions (by some measure) in the diet of the given amphibian ?

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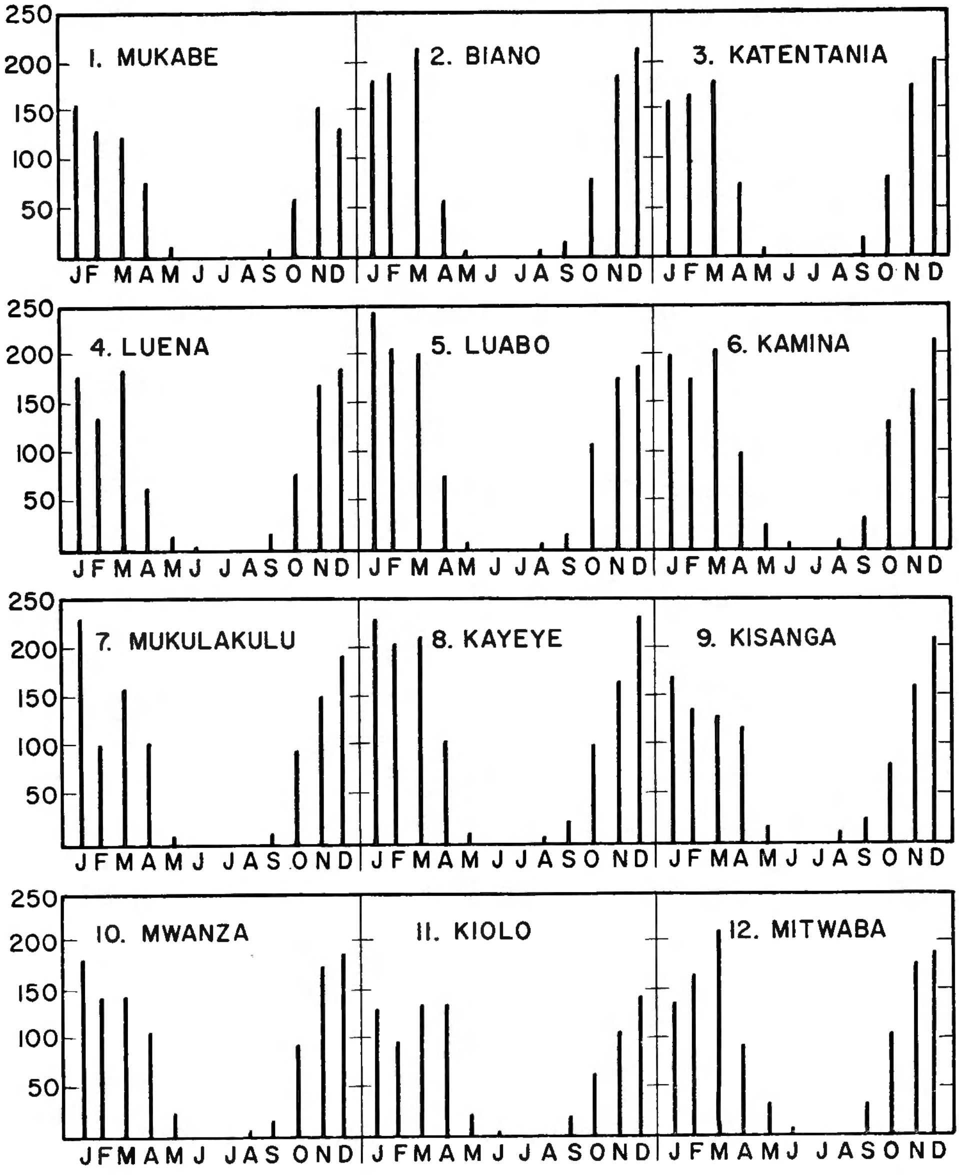

FIG. 1. — Average monthly rainfall (mm) of 12 stations surrounding the Parc National de l'Upemba.

Intra-specific variation in diet may be caused by seasonal or altitudinal changes. The abundance in the environment of a given prey may be drastically reduced during the five-month dry season. Winged imagos of *Isoptera* are almost unavailable to non-fossorial frogs from May through September. Terrestrial gastropods usually are not active during the dry season. Other invertebrates may be affected similarly. Altitude can have the same effect on prey distribution, especially in the Upemba with its total relief of about 1,300 m. As one type of prey becomes less available, an amphibian is obliged either to eat more of other kinds of prey or to reduce its food intake. Therefore, the taxonomic analysis outlined in the preceding paragraph must be carried out separately for each season and for each altitudinal zone. Ideally such analysis would be carried out separately for each month of the year and for every 50 or 100 m. Lack of material (see below, *material and methods*) restricted analysis to wet and dry seasons and to 250-meter altitudinal zones.

Seasonal and altitudinal changes may affect the diet as a whole without affecting the amounts eaten of any given prey. If, for example, a frog eats few *Isoptera* in the dry season, the proportions of the other important food categories increase relative to the wet season. But the actual amounts of *Coleoptera* eaten may remain constant. The seasonal and altitudinal variation of each important food type must be tested separately. For each species of amphibians, therefore, we asked the following questions : Is the amount of *Formicidae* (or any other prey) eaten at a particular elevation the same in wet and dry seasons ? Is the amount of *Formicidae* (or other food) eaten during the wet (or dry) season the same at all altitudes ?

As another potential source of intra-specific variation in diet is the size of the individual frogs, we should also ask if a correlation exists between snout-vent length of the frog and size of its prey.

These aspects of intra-specific variation in diet must be analyzed before interspecific variation is studied. For each genus the questions to be raised are : Do the diets of the various species fit a pattern ? Do the same prey categories make up the bulk of the food in each case ? Does each species eat the same amount of Coleoptera (or any other food type) ? Is the size of the species related to the size of its prey ?

The time of day at which feeding takes place, the proportion of stomachs containing food, and the changes in diet related to changes in habitat are aspects of the general problem of feeding behavior that cannot be analyzed in this study because of the lack of field data (see below).

Noble (1924) analyzed the stomach contents of a number of amphibians from the Congo. His analysis, however, did not consider seasonal variation and was limited to counts of the individuals of various prey categories. As will be shown below, such counts are probably the least satisfactory measure of dietary significance. Because of the difference in kind of measurement, comparison of our findings with Noble's would be meaningless and is not attempted. LOVERIDGE (1933, 1936, 1942) noted the food of a few species included in our report. As his data comprised the number of stomachs as well as the number of individual prey, LOVERIDGE's observations are more useful and will be referred to where appropriate.

MATERIALS AND METHODS.

The material used in this study was obtained by the Mission G. F. DE WITTE as part of the « Exploration du Parc National de l'Upemba ». During the intervals June-July, 1945, and February, 1945-July, 1949, the field party collected roughly 80,000 amphibians, of which about 75,000 were available to us. Unfortunately the data accompanying this well-preserved collection are limited to locality, date, and altitude. Because habitat and hour of collection were not recorded, certain questions (see above) concerning food and feeding habits cannot be dealt with.

Only the contents of stomachs were studied. Identification of the largely digested contents of intestines would have been limited to heavily sclerotized prey because of the more rapid decomposition of soft-bodied prey. To have used intestinal material, therefore, would have introduced a bias, giving undue weight to the organisms more likely to persist as fragments.

As each stomach was removed, the species, sex, and size of the frog were recorded on a 3 × 5 inch card. Each frog used was given an individual number, which was also recorded on the card and written on one tag placed in the body cavity and on another tag kept with the stomach. The stomachs were placed in separate vials and covered with seventy per cent ethyl alcohol, the same concentration in which the amphibians had been kept for several years.

All stomachs were opened later by means of fine scissors, the smaller stomachs under a binocular microscope. The contents of each stomach were washed with alcohol into Petri dishes. The names of the groups of food organisms, the number of each kind, their total lengths (in 0.5 mm), and their volumes were recorded on the card for that stomach.

In determining volumes, an identified food organism was placed in a cylinder graduated in 0.1 ml and seventy per cent ethyl alcohol run in from a burette, also graduated in 0.1 ml, to the nearest whole milleliter. The difference between the cylinder reading and the amount of alcohol removed from the burette gave the volume of the food organism. A volume determination for a single individual of a very small food species was impossible. In such instances the volume was estimated on the basis of several individuals (as few as 3, but usually more than 10) of the same species or of a related species of comparable size. For every group of food species a volume-length record was kept, thus facilitating estimation of isolated, small specimens. A symbol opposite each volume record indicated whether the volume was determined directly from the particular item or estimated from volume determinations of other related forms.

Identifications of insect food items were usually carried only to family level. In some groups, notably the termites, it was possible to obtain generic identifications readily. But to do so for the majority of forms would have required the efforts of numerous specialists and many years. Non-insect food was identified only to class or order depending on the state of preservation and the group involved. *Diplopoda*, for example, were identified only to class because to go beyond that level is the work of a specialist. Halting identification at the levels indicated limits the ecological information obtained; nevertheless, the major habitat type of the food organisms — whether aquatic or terrestrial — is obtainable. For example, no *Formicidae* or *Isoptera* are aquatic whereas all *Gerridae* are. Thus the major feeding habitat for each species of anuran can be determined from our identifications.

The contents of many stomachs were in two distinct stages of decomposition, indicating two distinct feedings. For example, the stomach of *Bufo regularis* 546-1 contained, among numerous other animals, 79 entire worker termites of the genus *Macrotermes*. It also contained the head capsules of 23 additional workers of the family *Termitidae*. Since the sclerotization of the worker termites of this family varies only slightly, the only explanation of the difference in states of decomposition is duration of time in the stomach. In such cases the classes of food were separated on the cards. Food organisms of the earlier feeding were represented by fragments that were so incomplete that identification usually could not be carried to customary levels. Frequently, beetles of an earlier feeding would be represented only by elytra and ants and termites only by head capsules.

The fragments of the earlier feedings were not used because the inclusion of such material would have introduced the same bias that intestinal material would (see above). The entire contents of some stomachs were in this advanced state of digestion and could not be used in our analysis.

In order to answer the questions concerning seasonal and altitudinal variation in the diets, an attempt was made to select 25 stomachs per species from each month and at every 50-100 m. Although the number of specimens in this collection is enormous, fluctuations in the activities of the frogs and peculiarities of topography of the park made it impossible to collect frogs (and, hence, stomachs) in an even distribution over the year and at every altitude. For some months no frogs were available, forcing the abandonment of a month by month analysis. Data for the dry months (May through September) were lumped as were those of the wet months, and a wet versus dry season analysis made. However, we still tried to obtain as many as 25 stomachs from each month.

As the grouping of elevations into zones in a previous report (SCHMIDT and INGER, 1959) introduced no illogical patterns, the same system was followed in this study. The altitudinal zones (in meters) used were : 585-750, 751-1,000, 1,001-1,250, 1,251-1,500, 1,501-1,750, 1,751-1,830. The The selection of monthly samples of stomachs was carried out in each of these zones as far as possible, and within each zone we tried to distribute the stomachs used over a number of localities.

The collection was stored by lots or series, each lot comprising the total individuals of a given species caught at a particular place and time. We did not formally randomize the selection of lots or individuals within lots, but simply started with any lot of a given species. Adult or subadult frogs were taken just as we came to them and their stomachs removed. Each stomach was partly slit; if it was empty, it was not used. As already noted, lack of precise habitat notes and hour of collection made empty stomachs worthless to this study.

Once all of the stomachs for a species had been examined, the data cards were arranged in numerical order, and 50 were selected by use of a table of random digits (WALLIS and ROBERTS, 1956) for testing the relationship between the sizes of predator and prey. For all other tests the grouping by seasons and altitudinal zones was maintained.

The quantity of data accumulated is too large to be presented in its entirety. The cards are being kept by the authors to whom all inquiries concerning the data should be addressed.

Quantitative analysis of the diets of predaceous animals may utilize several types of measurement : the number of stomachs in which a particular kind of prey occurs, or the number, volume, or weight of each type of food. All of these measurements are valuable. The number of stomachs is a measure of the effort a given species devotes to obtaining a given type of food. If pselaphid beetles appear in only one of 1,000 stomachs, their capture is only accidental, for whatever reason, compared to a food type that appears in 100 of the 1,000 stomachs. The species studied must spend more time eating the second type of food, which is definitely more important in the diet than *Pselaphidae*.

The other measurements are estimates of the energy contributions of each type of prey, the most important aspect of food if attention is focused on the predator. The number of items eaten is probably the least satisfactory estimate. Using this measurement, five small *Formicidae* would be five times as important as one medium-sized carabid beetle found in the same stomach, although it is most unlikely that the predator would derive as much energy from the *Formicidae* as from the *Carabidae*.

The best estimate of food value, next to calorimetric determinations, is probably weight. Weighing, however, has the disadvantage of requiring much time and, with material preserved in fluid, one has the additional problem of adjusting for the preservative. Although volume is not as good an estimate as weight, it can be determined quickly and the preservative introduces no problem.

For each of the questions posed in the Introduction we made the null hypothesis, i.e., that there was no difference between the classes of observations being compared, whether those classes were types of food, seasons, altitudes, or species of amphibians. The statistical tests appropriate to our data are non-parametric and are described by SIEGEL (1956).

As Siegel points out, parametric statistical tests, such as the *t* test and analysis of variance, assume that the observations being tested are independent, are drawn from normally distributed populations, and are drawn from populations having equal variances. Parametric statistics have greater power (that is, they increase the probability of rejecting the null hypothesis when it is in fact false) than non-parametric ones. But unless the three assumptions mentioned (and for some parametric statistics there are more) are satisfied, parametric statistics are not appropriate. The distributions and variances of the volumes of various prey are unknown and certain observations are not independent of one another. Thus none of the three assumptions of parametric statistics are satisfied by our data.

An outline of the tests applied is given here because they have not been used before in food studies. For the test of taxonomic uniformity of the diet of each species we used the Friedman two-way analysis of variance, a test applicable in cases of many samples that are related. The procedure for this test is as follows : each stomach of the given species from one season and altitudinal zone is listed in a table; the number of the stomach is listed in the left hand column and the volumes of the various types of food it contains are placed under columns headed by the names of the six to twelve types of food that appear most often; a second table having the same column headings as the first is constructed; in the second table the volumes within a particular stomach are assigned ranks, the largest volume receiving the rank of 10 (if we used that many types of food) and the smallest a rank of 1; the arithmetic operations of the Friedman test are carried out on the intra-stomach ranks. The two working tables are illustrated in Table 1. Note that the average rank is assigned in the case of ties, including zero values. Since each prey eaten by a frog affects the amount it can eat subsequently at the same « meal », the items within a stomach are not independent of one another. For that reason the Friedman analysis of variance of related observations is the appropriate test.

Seasonal variation was tested by the Mann-Whitney U test. All of the stomachs of a given species collected during the wet season at a given elevation are arranged in order according to the volume of, let us say, *Formicidae* they each contained, with the stomachs without *Formicidae* at the end. The dry season stomachs of that species and elevation are arranged in similar fashion. The volumes of *Formicidae*, including the zero values, are listed under « wet » and « dry season » columns, and ranks assigned to them without regard to column (Table 2). The arithmetic operations utilize the ranks. As in the preceding test, ties between columns

TABLE 1. — **The form of working tables used in Friedman two-way analysis of variance test of taxonomic uniformity of diet.**

Stomach number	*Isoptera*	*Formicidae*	*Coleoptera*	*Orthoptera*	*Diptera*	*Blattaria*	*Lepidoptera*	*Hemiptera*	*Araneida*	All others
					Volumes (ml).					
2369–9	0	0.002	0	0	0	0	0	0	0	0
2480–2	0	0.16	0	0.10	0.15	0	0.20	0	0.07	0
2481–2	0	0.006	0	0	0	0.03	0	0	0.07	0
					Ranked volumes.					
2369–9	5	10	5	5	5	5	5	5	5	5
2480–2	3	9	3	7	8	3	10	3	6	3
2481–2	4	8	4	4	4	9	4	4	10	4

are given averaged ranks. The same test was applied to any two independent samples being compared whether the comparison was of two seasons or two altitudinal zones in one species, or a comparison of two species of amphibians. Such samples are independent because what one stomach contains will not affect what another contains unless food supply is very limited.

In general, however, a given amphibian was represented by samples drawn from more than two altitudinal zones, and a genus of amphibians represented by more than two species. In such cases of multiple, independent samples, the Kruskal-Wallis analysis of variance test was applied. The arrangement of data is like that of the Mann-Whitney U test, differing only in that three or more columns (= samples) are used. Ranks are assigned to the volumes, as in the Mann-Whitney test, and are used in the arithmetic operations.

Correlations between the sizes of frog and prey were measured by means of the Spearman rank correlation coefficient. For each species, the 50 stomachs selected at random for this test (see above, p. 8) are listed in

TABLE 2. — **Form of working tables used in Mann-Whitney U test of seasonal variation in volume of *Formicidae* eaten.**

Wet season		Dry season	
Volumes (ml)	Rank	Volumes (ml)	Rank
0.082	19	0.148	21
0.08	18	0.129	20
0.077	17	0	5
0.071	16	0	5
0.021	15	0	5
0.014	14	0	5
0.008	13	0	5
0.005	12	0	5
0.005	11		
0.003	10		
0	5		
0	5		
0	5		

a table giving the snout-vent lengths of the frogs in one column and the average volume of the individual food items within each stomach in a second column opposite the appropriate snout-vent length. Ranks are assigned to the values in each column independently and the arithmetic operations carried out using the ranks. The statistical significance of the coefficient obtained can be determined by a t test. As a negative coefficient (i.e., the larger the frog, the smaller the food) has no biological meaning in this case, a single-tailed t test only of the positive coefficients is used. A negative coefficient is automatically considered as not significant.

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RESULTS

Family PIPIDAE.

Genus **XENOPUS** WAGLER.

Xenopus laevis.

Food-containing stomachs of 180 frogs were examined; they had the following distribution :

Meters	585-750	751-1,000	1,001-1,250	1,501-1,750	1,751-1,830
Wet season	37	—	28	24	36
Dry season	9	27	—	—	19

The taxonomic distribution of the food is given in Table 3. The abundance of aquatic organisms is striking and exceeds that observed in other Upemba amphibians. Specimen 982-3 (30.7 mm) was typical and contained one newly metamorphosed frog, one *Odonata* nymph, 1 *Notonectidae*, one tabanid larva, and one chironomid larva — all aquatic forms. All of the *Ephemerida* and *Odonata* eaten were aquatic immature stages. All of the *Culicidae* (in 18 stomachs) and all but three of *Chironomidae* (in 20 stomachs) were aquatic larvae. Fifteen stomachs contained dytiscid beetles, whereas only 5 contained the generally much more abundant *Carabidae*. Twenty-one of the 35 specimens containing amphibians had eaten tadpoles and six others had eaten egg masses. Only in the stomachs of this species were copepods and ostracods found. *Xenopus* not only feeds on aquatic organisms, but also feeds in the water (ROSE, 1950) as do its relatives *Pipa* (RABB and SNEDIGAR, 1960) and *Hymenochirus*.

Eight stomachs, all from one lot, each contained one small, newly hatched bird. Presumably a nest had fallen into the water.

The presence of terrestrial prey (e.g., *Formicidae*) cannot be explained solely by these organisms falling into water accidentally, for *Xenopus* does leave the water to wander overland and may feed at such times.

The diet deviated from uniformity significantly in four of the seven zones tested (Table 4). In those four, *Coleoptera*, *Diptera*, and *Amphibia* were eaten in greatest volumes.

Almost no seasonal variation in diet was found (Table 5) in the two altitudinal zones at which it could be tested. *Formicidae* and *Hemiptera* were eaten in larger volumes in the dry season at one altitudinal zone each.

TABLE 3. — **Taxonomic distribution of prey in 180 stomachs of** *Xenopus laevis* **from the Parc National de l'Upemba.**

Numbers of stomachs containing principal food types given in parentheses.

ANNELIDA. — **Oligochaeta** (18).

MOLLUSCA.
- **Gastropoda.**
- **Pelycopoda.**

ARTHROPODA.
- **Crustacea.**
  - *Copepoda.*
  - *Decapoda.*
  - *Isopoda.*
  - *Ostracoda.*
- **Arachnida.** — *Araneida* (11).
- **Diplopoda.**
- **Insecta.**
  - *Ephemerida* (20).
  - *Odonata* (20).
    - *Anisoptera.*
    - *Coenagrionidae.*
    - *Gomphidae.*
    - *Lestidae.*
    - *Libellulidae.*
  - *Blattaria.*
  - *Orthoptera* (18).
    - *Gryllidae.*
    - *Gryllotalpidae.*
    - *Phasmatidae.*
    - *Tetrigidae.*
  - *Dermaptera.*
  - *Isoptera.* — *Termitidae* (16).
  - *Hemiptera* (34).
    - *Belastomatidae.*
    - *Cicadellidae.*
    - *Corixidae.*
    - *Fulgoridae.*
    - *Gerridae.*
    - *Hydrometridae.*
    - *Naucoridae.*
    - *Notonectidae.*
    - *Ochteridae.*
    - *Pleidae.*
    - *Reduviidae.*
  - *Trichoptera.* — *Rhyacophilidae.*
  - *Lepidoptera* (10).
  - *Diptera* (55).
    - *Ceratopogonidae.*
    - *Chironomidae.*
    - *Culicidae.*
    - *Ephydridae.*
    - *Nematocera.*
    - *Sciaridae.*
    - *Stratiomyidae.*
    - *Tabanidae.*
  - *Coleoptera* (53).
    - *Carabidae.*
    - *Chrysomelidae.*
    - *Coccinellidae.*
    - *Curculionidae.*
    - *Dytiscidae.*
    - *Elateridae.*
    - *Gyrinidae.*
    - *Helodidae.*
    - *Histeridae.*
    - *Hydrophilidae.*
    - *Scarabaeidae.*
    - *Staphylinidae.*
  - *Hymenoptera.*
    - *Apoidea.*
    - *Aulacridae.*
    - *Chalcidoidea.*
    - *Formicidae* (27).

CHORDATA.
- **Pisces.**
- **Amphibia** (35).
- **Aves.**

Altitudinal variation was more extensive (Table 6) and involved all of the prey categories tested.

The average volume of individual prey organisms within each of 50 stomachs chosen at random varied from 0.001 to 4.95 ml (median 0.018), which was the same range as total volume in these stomachs. The number of items in each stomach varied from 1 to 88. Thirteen stomachs contained one item, nine contained 2, thirteen 3 to 5, seven 6 to 10, four 13 to 20, two 21 to 30, and one 88.

TABLE 4. — **Test of uniformity of diet of** *Xenopus laevis* **from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	*0.01*	*Amphibia, Coleoptera, Orthoptera*
585– 750	Dry	0.45	*Formicidae, Coleoptera, Hemiptera*
751–1,000	Dry	0.13	*Diptera, Formicidae, Orthoptera*
1,001–1,250	Wet	*0.006*	*Formicidae, Diptera, Coleoptera*
1,501–1,750	Wet	< *0.001*	*Diptera, Amphibia, Coleoptera*
1,751–1,830	Wet	*0.016*	*Coleoptera, Isoptera, Annelida*
1,751–1,830	Dry	0.21	*Odonata, Hemiptera, Annelida*

TABLE 5. — **Seasonal variation in volumes of given prey eaten by** *Xenopus laevis* **in the Parc National de l'Upemba.**

Probabilities for statistically significant variation are in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	585– 750	*0.002*	Dry
Formicidae	1,751–1,830	0.9	Dry
Coleoptera	585– 750	0.96	Wet
Coleoptera	1,751–1,830	0.056	Wet
Hemiptera	585– 750	0.74	Dry
Hemiptera	1,751–1,830	*0.02*	Dry
Orthoptera	585– 750	0.58	Wet
Orthoptera	1,751–1,830	0.9	Dry
Diptera	585– 750	0.11	Dry
Diptera	1,751–1,830	0.42	Dry
Amphibia	585– 750	0.26	Wet
Amphibia	1,751–1,830	0.64	Dry

TABLE 6. — **Altitudinal variation in volumes of given prey eaten by** *Xenopus laevis* **in the Parc National de l'Upemba.**

Probabilities for statistically significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	0.42	1,001-1,250
Formicidae	Dry	*0.02*	585- 750
Coleoptera	Wet	*0.02*	1,751-1,830
Coleoptera	Dry	*0.05*	585- 750
Hemiptera	Wet	0.85	1,501-1,750
Hemiptera	Dry	*0.05*	1,751-1,830
Diptera	Wet	< *0.001*	1,501-1,750
Diptera	Dry	0.35	751-1,000
Amphibia	Wet	< *0.001*	1,501-1,750
Amphibia	Dry	0.70	1,751-1,830

Snout-vent lengths of these 50 frogs measured 30.7-69.6 mm (median 47.0) and were not correlated with average volume of individual prey (Spearman rank coefficient +0.082; t=0.57; P=0.57).

Family **BUFONIDAE.**

Genus **BUFO** LAURENTI.

Bufo regularis.

The 235 stomachs examined had the following distribution :

Meters	585-750	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	126	15	18	3	11	6
Dry season	30	11	5	6	—	4

The taxonomic distribution of the food is given in Table 7.

Statistically significant deviations from uniformity of diet appeared in almost every season and altitude tested (Table 8). *Formicidae* and *Coleoptera* were by far the most important types of food with *Isoptera*

TABLE 7. — **Taxonomic distribution of food occuring in 235 stomachs of** *Bufo regularis* **collected in the Parc National de l'Upemba.**

Number of stomachs containing principal groups given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.
- *Acarina.*
- *Araneida* (30).
- *Phalangida.*
- *Scorpionida.*

Diplopoda (24).

Chilopoda.
- *Geophilomorpha.*

Insecta.
- *Odonata.* — *Gomphidae.*
- *Blattaria.*
- *Orthoptera* (23).
  - *Acrididae.*
  - *Gryllidae.*
  - *Tetrigidae.*
  - *Tettigoniidae.*
  - *Tridactylidae.*
- *Dermaptera.*
- *Embioidea.*
- *Isoptera.* — *Termitidae* (68).
- *Corrodentia.*
- *Hemiptera* (22).
  - *Aradidae.*
  - *Cicadellidae.*
  - *Cydnidae.*
  - *Fulgoridae.*
  - *Gerridae.*
  - *Hydrometridae.*
  - *Lygaeidae.*
  - *Pentatomidae.*
  - *Plataspidae.*
  - *Reduviidae.*
- *Lepidoptera* (20).
  - *Noctuidae.*
- *Diptera* (12).
  - *Chironomidae.*
  - *Cyclorrhapha.*
  - *Drosophilidae.*
  - *Mycetophilidae.*
  - *Psychodidae.*
  - *Stratiomyidae.*
  - *Syrphidae.*
- *Coleoptera* (160).
  - *Brenthidae.*
  - *Carabidae.*
  - *Cerambycidae.*
  - *Chrysomelidae.*
  - *Cicindelidae.*
  - *Dytiscidae.*
  - *Elateridae.*
  - *Erotylidae.*
  - *Histeridae.*
  - *Hydrophilidae.*
  - *Nitidulidae.*
  - *Omophronidae.*
  - *Ostomatidae.*
  - *Paussidae.*
  - *Pselaphidae.*
  - *Scarabaeidae.*
  - *Scolytidae.*
  - *Staphylinidae.*
  - *Tenebrionidae.*
- *Hymenoptera.*
  - *Apidae.*
  - *Braconidae.*
  - *Chalcidoidea.*
  - *Euchariidae.*
  - *Formicidae* (204).
  - *Ichneumonidae.*
  - *Mutillidae.*
  - *Sphecidae.*

CHORDATA.

Amphibia.
- *Arthroleptis stenodactylus* (1).
- *Leptopelis* sp. (1).

Reptilia.
- *Scincidae* (1).

TABLE 8. — **Test of uniformity of diet of *Bufo regularis* from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	< *0.001*	*Formicidae, Coleoptera, Isoptera*
585– 750	Dry	< *0.001*	*Formicidae, Coleoptera, Araneida*
751–1,000	Wet	< *0.001*	*Formicidae, Isoptera, Coleoptera*
751–1,000	Dry	0.08	*Formicidae, Coleoptera, Isoptera*
1,001–1,250	Wet	< *0.001*	*Formicidae, Coleoptera, Isoptera*
1,001–1,250	Dry	*0.01*	*Formicidae, Coleoptera, Orthroptera*
1,251–1,500	Wet	0.17	*Coleoptera, Formicidae, Diplopoda*
1,251–1,500	Dry	*0.04*	*Formicidae, Lepidoptera, Coleoptera*
1,501–1,750	Wet	*0.01*	*Coleoptera, Formicidae*
1,751–1,830	Wet	0.07	*Coleoptera, Formicidae, Diptera*
1,751–1,830	Dry	*0.05*	*Formicidae, Coleoptera, Araneida*

a major, though less important, element at lower elevations. The food was almost exclusively terrestrial. Even the amphibians eaten (*Arthroleptis stenodactylus* and *Leptopelis*) were non-aquatic. The only aquatic prey eaten occurred in very few stomachs : *Gerridae* 1, *Hydrometridae* 1, *Dytiscidae* 2, *Hydrophilidae* 3.

Little seasonal variation was shown by this sample (Table 9). *Isoptera* (neuter castes only) were eaten in larger volumes during the wet season in the lowest altitudinal zone. No pattern emerges from the seasonal variation in *Formicidae* eaten.

Only *Formicidae*, *Coleoptera*, and *Isoptera* were eaten in sufficient quantities at enough elevations to warrant testing of altitudinal variation. As Table 10 shows, little variation of this type appeared. The greater amount of *Isoptera* eaten at the lowest elevations is associated with greater abundance at those levels.

In 50 stomachs chosen at random from the sample, the average volume of food organisms varied from 0.001 to 0.158 ml (median 0.024). The total volume of food in these stomachs varied from 0.002 (1 item) to 13.31 ml (84 items). The maximum number of items in a stomach was 156, four containing one item, four 2, five 3 to 5, twelve 6 to 10, seven 11 to 20, five 21 to 30, five 31 to 50, and eight more than 50.

TABLE 9. — **Seasonal variation in volumes of given prey eaten by** *Bufo regularis* **in the Parc National de l'Upemba.**

Probabilities for statistically significant variations in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	585– 750	*0.015*	Wet
Formicidae	751–1,000	> 0.10	Wet
Formicidae	1,001–1,250	> 0.10	Dry
Formicidae	1,751–1,830	*0.02*	Dry
Coleoptera	585– 750	0.88	—
Coleoptera	751–1,000	> 0.10	Wet
Coleoptera	1,001–1,250	> 0.10	Dry
Coleoptera	1,751–1,830	0.45	Wet
Isoptera	585– 750	*0.002*	Wet
Isoptera	751–1,000	> 0.10	Wet
Isoptera	1,001–1,250	> 0.10	Wet
Araneida	585– 750	0.14	Dry
Hemiptera	585– 750	0.80	Dry

TABLE 10. — **Altitudinal variation in volumes of given prey eaten by** *Bufo regularis* **in the Parc National de l'Upemba.**

Probabilities for statistically significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	*0.03*	751–1,000
Formicidae	Dry	0.46	1,001–1,250
Coleoptera	Wet	0.21	1,751–1,830
Coleoptera	Dry	0.14	1,001–1,250
Isoptera	Wet	*0.01*	585– 750

Snout-vent lengths of the 50 toads from which these stomachs were taken ranged from 42.0 to 99.9 mm (median 59.1 mm). Snout-vent length was not correlated with the average volume of individual prey within stomachs (Spearman rank coefficient −0.035).

Bufo funereus.

The 242 stomachs examined had the following distribution :

Meters	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	6	7	8	23	58
Dry season	13	33	29	26	39

The taxonomic distribution of the food is given in Table 11.

The diet deviated significantly from uniformity at almost every elevation and season (Table 12). *Formicidae* and *Coleoptera* were by far the most important types of prey eaten by *funereus*. The other orders listed in Table 12 were eaten in much smaller quantities.

TABLE 11. — **Taxonomic distribution of food contained in 242 stomachs of** *Bufo funereus* **collected in the Parc National de l'Upemba.**

Number of stomachs containing principal groups given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.
- *Acarina.*
- *Araneida* (57).
- *Chelonethida.*
- *Phalangida.*

Diplopoda (29).

Chilopoda.
- *Geophilomorpha.*
- *Scolopendridae.*

Insecta.
- *Collembola.*
- *Odonata.*
- *Blattaria.*
- *Orthoptera* (15).
  - *Gryllidae.*
  - *Gyllotalpidae.*
  - *Tetrigidae.*
  - *Tettigoniidae.*
- *Dermaptera.*
- *Isoptera.* — *Termitidae* (18).
- *Hemiptera* (74).
  - *Aphididae.*
  - *Cicadellidae.*
  - *Coreidae.*
  - *Cydnidae.*
  - *Fulgoridae.*
  - *Heniocephalidae.*
  - *Hydrometridae.*
  - *Lygaeidae.*
  - *Membracidae.*
  - *Miridae.*
  - *Naucoridae.*
  - *Nepidae.*
  - *Ochteridae.*
  - *Pentatomidae.*
  - *Ploiariidae.*
  - *Reduviidae.*
  - *Tingidae.*
  - *Veliidae.*
- *Neuroptera.* — *Hemerobiidae.*
- *Trichoptera.* — *Hydropsychidae.*
- *Lepidoptera* (44).
  - *Geometridae.*

Diptera (40).
- *Bibionidae.*
- *Ceratopogonidae.*
- *Chironomidae.*
- *Cyclorrhapha.*
- *Diopsidae.*
- *Dixidae.*
- *Drosophilidae.*
- *Mycetophilidae.*
- *Phoridae.*
- *Psychodidae.*
- *Sciaridae.*
- *Stratiomyidae.*
- *Syrphidae.*
- *Tipulidae.*
- *Trypetidae.*

Coleoptera (186).
- *Bostrichidae.*
- *Buprestidae.*
- *Carabidae.*
- *Cerambycidae.*
- *Chrysomelidae.*
- *Cicindelidae.*
- *Cistelidae.*
- *Coccinellidae.*
- *Curculionidae.*
- *Dytiscidae.*
- *Elateridae.*
- *Elmidae.*
- *Endomychidae.*
- *Erotylidae.*
- *Histeridae.*
- *Hydrophilidae.*
- *Lagriidae.*
- *Lampyridae.*
- *Limnichidae.*
- *Melandryidae.*
- *Mordellidae.*
- *Nitidulidae.*
- *Omophronidae.*
- *Pselaphidae.*
- *Scarabaeidae.*
- *Scydmaenidae.*
- *Silphidae.*
- *Staphylinidae.*
- *Tenebrionidae.*

Hymenoptera.
- *Braconidae.*
- *Chalcidoidea.*
- *Formicidae* (194).
- *Mymarommatidae.*
- *Pterostigmatidae.*

CHORDATA.

Amphibia. — *Phrynobatrachus anotis* (1).

TABLE 12. — **Test of uniformity of diet of** *Bufo funereus* **from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
751–1,000	Wet	*0.03*	*Formicidae, Coleoptera, Araneida*
751–1,000	Dry	*0.005*	*Coleoptera, Formicidae, Hemiptera*
1,001–1,250	Wet	0.09	*Coleoptera, Formicidae, Araneida*
1,001–1,250	Dry	< *0.001*	*Coleoptera, Formicidae, Hemiptera*
1,251–1,500	Wet	< *0.001*	*Coleoptera, Formicidae, Diplopoda*
1,251–1,500	Dry	< *0.001*	*Formicidae, Coleoptera, Hemiptera*
1,501–1,750	Wet	< *0.001*	*Formicidae, Coleoptera, Hemiptera*
1,501–1,750	Dry	< *0.001*	*Formicidae, Coleoptera, Lepidoptera*
1,751–1,830	Wet	< *0.001*	*Coleoptera, Formicidae, Lepidoptera*
1,751–1,830	Dry	< *0.001*	*Formicidae, Coleoptera, Hemiptera*

TABLE 13. — **Seasonal variation in volumes of given prey eaten by** *Bufo funereus* **in the Parc National de l'Upemba.**

Probabilities for statistically significant variation in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	751-1,000	*0.003*	Wet
Formicidae	1,001-1,250	0.60	Wet
Formicidae	1.251-1,500	0.80	Wet
Formicidae	1,501-1,750	*0.011*	Wet
Formicidae	1,751-1,830	*0.008*	Wet
Coleoptera	751-1,000	> 0.10	Wet
Coleoptera	1,001-1,250	0.81	Dry
Coleoptera	1,251-1,500	0.17	Wet
Coleoptera	1,501-1,750	< *0.001*	Wet
Coleoptera	1,751-1,830	*0.007*	Wet
Hemiptera	751-1,000	> 0.10	Wet
Hemiptera	1,001-1,250	0.068	Dry
Hemiptera	1,251-1,500	0.13	Dry
Hemiptera	1,501-1,750	0.31	Wet
Hemiptera	1,751-1,830	0.28	Dry
Araneida	751-1,000	> 0.10	Wet
Araneida	1,001-1,250	0.92	—
Araneida	1,251-1,500	*0.045*	Wet
Araneida	1,501-1,750	0.74	Wet
Araneida	1,751-1,830	0.9	—

The prey of *funereus* is almost exclusively terrestrial. Approximately half (8 of 18) of the stomachs containing *Isoptera* had only neuter castes. Each of the following aquatic types appeared in one stomach : *Odonata*, *Hydrometridae*, *Trichoptera*, *Dytiscidae*, and *Elmidae*. The aquatic hemipterans *Nepidae* were found in three stomachs, and hydrophilid beetles in 21.

TABLE 14. — **Altitudinal variation in volumes of given prey eaten by *Bufo funereus* in the Parc National de l'Upemba.**

Probabilities for statistically significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	0.68	1,251-1,500
Formicidae	Dry	$<$ *0.001*	1,251-1,500
Coleoptera	Wet	0.68	1,251-1,500
Coleoptera	Dry	0.18	1,001-1,250
Hemiptera	Wet	0.50	751-1,000
Hemiptera	Dry	*0.011*	1,001-1,250
Araneida	Wet	0.10	1,001-1,250
Araneida	Dry	0.76	1,001-1,250

Seasonal variation (Table 13) was almost restricted to the *Formicidae*. Only the four orders listed in Table 13 were found in enough stomachs to make calculations worthwhile. Altitudinal variation in the diet was minor (Table 14).

In 50 stomachs chosen at random from the sample, the average volume of individual prey varied from 0.001 to 0.213 ml (median 0.014). The total of food in these stomachs ranged between 0.002 (1 item) and 2.19 mil (205 items). The maximum number of prey in one stomach was 263. Four stomachs contained one item, six 2, four 3 to 5, nine 6 to 10, six 11 to 20, five 21 to 30, seven 31 to 50, and nine more than 50.

Snout-vent lengths of these 50 toads varied from 40.3 to 62.9 mm (median 47.2 mm). Snout-vent length had a correlation of +0.224 (Spearman rank coefficient) with average volume of individual prey though the statistical significance of the coefficient is doubtful ($P=0.06$).

Bufo ushoranus.

The sample consisted of 10 stomachs from the wet season at 751-1,000 m and 9 from the wet season at 1,251-1,500 m.

The taxonomic distribution of the prey is given in Table 15. Only terrestrial organisms were eaten. At both altitudes the diet deviated significantly ($P < 0.001$) from uniformity. *Formicidae*, *Isoptera*, and

TABLE 15. — **Taxonomic distribution of food in 19 stomachs of** *Bufo ushoranus* **from the Parc National de l'Upemba.**

Number of stomachs containing principal categories given in parentheses.

MOLLUSCA. — **Gastropoda** (1).

ARTHROPODA.

Arachnida.

Acarina (6).
Chelonethida (1).

Insecta.

Collembola (3).
Isoptera. — *Termitidae* (12).
Hemiptera (1).
Lepidoptera (1).
Colleoptera (9).
Carabidae.
Chrysomelidae.
Cossyphodidae.
Curculionidae.
Elateridae.
Histeridae.
Pselaphidae.
Scarabaeidae.
Staphylinidae.
Hymenoptera.
Chalcidoidea.
Formicidae (18).

Coleoptera dominated the diet in that order of importance. Approximately one-third of the *Isoptera* eaten were imagos.

Seasonal variation could not be tested. The volumes of *Formicidae*, *Isoptera*, and *Cóleptera* eaten were approximately equal in the two altitudinal zones.

The average volume of individual prey varied from 0.0010 to 0.0228 ml (median 0.0027 ml). The total volume of food varied from 0.009 (8 items) to 0.434 ml (19 items). Five stomachs contained 7 to 10 items, four 11 to 20, four 21 to 30, four 31 to 50, one 122, and one 128.

Snout-vent lengths of these toads had a range of 20.1-25.0 mm (median 23.0 mm). Snout-vent length was not correlated with the average volume of prey within stomachs (Spearman rank coefficient +0.063).

Bufo melanopleura.

Only 36 stomachs, from toads collected in the wet season at 1,251-1,500 m, were studied.

The taxonomic distribution of the food is given in Table 16. Except for one hydrophilid beetle, all organisms eaten were terrestrial. The diet deviated significantly ($P < 0.001$) from uniformity. *Formicidae* and *Coleoptera* were the most important food categories with *Isoptera* (soldiers and workers only) and *Acarina* of secondary importance.

Seasonal and altitudinal variation could not be tested.

The average volume of individual prey varied from 0.0005 to 0.0061 ml (median 0.0013). The total volume of food per stomach ranged between 0.010 (9 items) and 0.196 ml (44 items). Of the 36 stomachs, one held 5 items, two 9 to 10, three 11 to 20, five 21 to 30, nine 31 to 50, and sixteen 51 to 129.

TABLE 16.

Taxonomic distribution of food contained in 36 stomachs of *Bufo melanopleura* **collected in the Parc National de l'Upemba.**

Number of stomachs containing principal groups given in parentheses.

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.
Acarina (19).
Araneida (6).
Phalangida.

Diplopoda (4).

Chilopoda.

Insecta.
Collembola (8).
Isoptera. — *Termitidae* (11).
Thysanoptera.
Hemiptera.
Aphididae.
Lepidoptera.
Diptera.
Coleoptera (34).
Byrrhidae.
Carabidae.
Chrysomelidae.
Curculionidae.
Elateridae.
Hydrophilidae.
Pselaphidae.
Scarabaeidae.
Scydmaenidae.
Staphylinidae.
Throscidae.
Hymenoptera.
Chalcidoidea.
Formicidae (36).

Snout-vent lengths of these toads varied from 16.3 to 25.1 mm (median 21.2). The correlation of snout-vent with average volume of prey was +0.258 (Spearman rank coefficient). The statistical significance of this coefficient is doubtful (P = 0.06).

SUMMARY OF BUFO SPECIES.

All four species fed heavily on *Formicidae* and *Coleoptera* (Table 17). This concentration on the two foods has the effect of reducing altitudinal and seasonal variation (Tables 18 and 19), as the secondary foods were usually not present in enough stomachs to have an effect on statistical calculations.

Of the seven seasonal-altitudinal zones in which comparison of *regularis* and *funereus* was possible, they differ significantly (P = 0.05) in volumes of *Formicidae* eaten in three and in volumes of *Colepotera* eaten in two (Table 20). But direction of difference is not significant as either species may consume more of either prey than the other.

The two smaller species, *melanopleura* and *ushoranus*, ate more *Isoptera* and*Acarina* than did *regularis* and *funereus* (Table 20). Selectivity, as well as availability, plays a role in predation, for *Acarina* were not eaten by the small species of *Phrynobatrachus* (p. 66) to the same extent though both

TABLE 17. — **Significant deviations from uniformity in diets of species of *Bufo* from the Parc National de l'Upemba.**

Species	Altitude	Season	Dominant food
regularis	585– 750	Wet	*Formicidae, Coleoptera, Isoptera*
regularis	585– 750	Dry	*Formicidae, Coleoptera, Araneida*
regularis	751–1,000	Wet	*Formicidae, Isoptera, Coleoptera*
funereus	751–1,000	Wet	*Formicidae, Coleoptera, Araneida*
ushoranus	751–1,000	Wet	*Formicidae, Isoptera, Coleoptera*
funereus	751–1,000	Dry	*Coleoptera, Formicidae, Hemiptera*
regularis	1,001–1,250	Wet	*Formicidae, Coleoptera, Isoptera*
regularis	1,001–1,250	Dry	*Formicidae, Coleoptera, Orthoptera*
funereus	1,001–1,250	Dry	*Coleoptera, Formicidae, Hemiptera*
funereus	1,251–1,500	Wet	*Coleoptera, Formicidae, Diplopoda*
ushoranus	1,251–1,500	Wet	*Formicidae, Isoptera, Coleoptera*
melanopleura	1,251–1,500	Wet	*Formicidae, Coleoptera, Isoptera*
regularis	1,251–1,500	Dry	*Formicidae, Lepidoptera, Coleoptera*
funereus	1,251–1,500	Dry	*Formicidae, Coleoptera, Hemiptera*
funereus	1,501–1,750	Wet	*Formicidae, Coleoptera, Hemiptera*
regularis	1,501–1,750	Wet	*Coleoptera, Formicidae*
funereus	1,501–1,750	Dry	*Formicidae, Coleoptera, Lepidoptera*
funereus	1,751–1,830	Wet	*Coleoptera, Formicidae, Lepidoptera*
funereus	1,751–1,830	Dry	*Formicidae, Coleoptera, Hemiptera*
regularis	1,751–1,830	Dry	*Formicidae, Coleoptera, Araneida*

genera of amphibians occur in the same habitats. Presumably *Isoptera* were equally available to all four species of *Bufo* at a given altitude, yet were eaten in greater quantities by the two smaller species.

The size of the prey of the four species of *Bufo* differs significantly (Table 71). The Kruskal-Wallis test applied to the data referred to in each species' account shows that the null hypothesis may be rejected ($H = 85.77$; $P < 0.001$). Although within each species the correlation

TABLE 18.

Significant seasonal variation in quantities of given prey eaten by species of *Bufo* in the Parc National de l'Upemba.

Species	Altitude	Food	Season of greater consumption
regularis	585– 750	*Formicidae*	Wet
regularis	585– 750	*Isoptera*	Wet
funereus	751–1,000	*Formicidae*	Wet
funereus	1,251–1,500	*Araneida*	Wet
funereus	1,501–1,750	*Formicidae*	Wet
funereus	1,501–1,750	*Coleoptera*	Wet
regularis	1,751–1,830	*Formicidae*	Dry
funereus	1,751–1,830	*Formicidae*	Wet
funereus	1,751–1,830	*Coleoptera*	Wet

TABLE 19.

Significant altitudinal variation in the volumes of given prey eaten by species of *Bufo* in the Parc National de l'Upemba.

Species	Season	Food	Altitude of maximum consumption
regularis	Wet	*Formicidae*	751–1,000
regularis	Wet	*Isoptera*	585– 750
funereus	Dry	*Hemiptera*	1,001–1,250
funereus	Dry	*Formicidae*	1,251–1,500

between snout-vent length of the toad and average volume of food items is not statistically significant, a positive correlation exists between species (Table 71). The interspecies correlation between food size and number of items per stomach is negative.

TABLE 20. — **Significant differences among species of *Bufo* in the Parc National de l'Upemba in volumes of given prey eaten.**

Prey	Altitude	Season	P	*Species compared,* in order of decreasing consumption
Formicidae	751-1,000	Dry	0.05	*regularis, funereus*
Coleoptera	751-1,000	Dry	0.05	*funereus, regularis*
Formicidae	1,001-1,250	Dry	0.005	*regularis, funereus*
Isoptera	1,251-1,500	Wet	0.026	*ushoranus, melanopleura, regularis, funereus*
Coleoptera	1,251-1,500	Wet	0.005	*regularis, funereus, melanopleura, ushoranus*
Acarina	1,251-1,500	Wet	0.02	*melanopleura, ushoranus, regularis, funereus*
Formicidae	1,501-1,750	Wet	0.009	*funereus, regularis*

Family RANIDAE.

Genus RANA LINNAEUS.

Rana fuscigula.

Stomachs containing food were removed from 273 frogs having the following distribution :

Meters	585-750	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	3	14	56	21	45	8
Dry season	3	13	42	15	39	14

The taxonomic distribution of the food is given in Table 21. The diet consisted primarily of large, active, terrestrial arthropods. Though *Formicidae* were present in many stomachs, they were not as heavily represented in the diet as their abundance in the fauna would lead them to be if simple availability determined the diet of *fuscigula*. Aquatic food was relatively insignificant. *Odonata* occurred in four stomachs, aquatic *Hemiptera* (*Belastomatidae*, *Hydrometridae*, and *Nepidae*) in five, aquatic *Coleoptera* (*Dytiscidae* and *Hydrophilidae*) in three, and amphibians in eleven.

TABLE 21. — **Taxonomic distribution of prey found in 273 stomachs of** *Rana fuscigula* **from the Parc National de l'Upemba.**

Numbers of stomachs containing principal food types given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda** (38).

ARTHROPODA.

- **Crustacea.** — Isopoda.
- **Arachnida.**
  - *Acarina.*
  - *Araneida* (69).
  - *Phalangida.*
- **Chilopoda.**
  - *Geophilomorpha.*
- **Diplopoda.**
- **Insecta.**
  - *Odonata.*
    - *Libellulidae.*
  - *Blattaria* (21).
  - *Orthoptera* (68).
    - *Acrididae.*
    - *Gryllidae.*
    - *Gryllotalpidae.*
    - *Manteidae.*
    - *Phasmidae.*
    - *Stenopalmatidae.*
    - *Tetrigidae.*
    - *Tettigoniidae.*
  - *Dermaptera.*
  - *Isoptera.* — *Termitidae.*
  - *Hemiptera* (80).
    - *Aphididae.*
    - *Aradidae.*
    - *Belastomatidae.*
    - *Cicadellidae.*
    - *Coreidae.*
    - *Cydnidae.*
    - *Fulgoridae.*
    - *Henicocephalidae.*
    - *Hydrometridae.*
    - *Lygaeidae.*
    - *Naucoridae.*
    - *Nepidae.*
    - *Ochteridae.*
    - *Pentatomidae.*
    - *Ploiariidae.*
    - *Reduviidae.*
    - *Saldidae.*
    - *Scutelleriidae.*
  - *Lepidoptera* (91).
  - *Diptera* (27).
    - *Anthomyidae.*
    - *Brachycera.*
    - *Calliphoridae.*
    - *Cyclorrhapha.*
    - *Diopsidae.*
    - *Sciariidae.*
    - *Stratiomyidae.*
    - *Syrphidae.*
    - *Tabanidae.*
    - *Tipulidae.*
    - *Trypetidae.*
  - *Coleoptera* (129).
    - *Carabidae.*
    - *Cerambycidae.*
    - *Chrysomelidae.*
    - *Cicindelidae.*
    - *Cistelidae.*
    - *Coccinellidae.*
    - *Curculionidae.*
    - *Dytiscidae.*
    - *Elateridae.*
    - *Endomychidae.*
    - *Erotylidae.*
    - *Hydrophilidae.*
    - *Lagridae.*
    - *Limnichidae.*
    - *Psephenidae.*
    - *Scarabaeidae.*
    - *Staphylinidae.*
    - *Tenebrionidae.*
  - *Hymenoptera.*
    - *Apidae.*
    - *Braconidae.*
    - *Chalcidoidea.*
    - *Formicidae* (85).
    - *Ichneumonidae.*
    - *Tenthredinidae.*
    - *Vespidae.*

CHORDATA. — **Amphibia** (11).

TABLE 22. — **Test of uniformity of diet of** *Rana fuscigula* **from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
751–1,000	Wet	0.86	*Lepidoptera, Coleoptera, Mollusca*
751–1,000	Dry	0.30	*Formicidae, Coleoptera, Diptera*
1,001–1,250	Wet	< *0.001*	*Coleoptera, Orthoptera, Formicidae*
1,001–1,250	Dry	0.10	*Hemiptera, Orthoptera, Formicidae*
1,251–1,500	Wet	0.28	*Orthoptera, Coleoptera, Lepidoptera*
1,251–1,500	Dry	0.46	*Araneida, Coleoptera, Lepidoptera*
1,501–1,750	Wet	< *0.001*	*Lepidoptera, Coleoptera, Araneida*
1,501–1,750	Dry	*0.005*	*Coleoptera, Hemiptera, Araneida*
1,751–1,830	Wet	0.87	*Lepidoptera, Mollusca, Coleoptera*
1,751–1,830	Dry	0.28	*Hemiptera, Coleoptera, Lepidoptera*

TABLE 23. — **Statistically significant seasonal variation in the volumes of given prey eaten by** *Rana fuscigula* **in the Parc National de l'Upemba.**

Prey	Altitude	P	Season of greater consumption
Mollusca	751–1,000	0.04	Wet
Mollusca	1,501–1,750	< 0.001	Wet
Mollusca	1,751–1,830	0.03	Wet
Coleoptera	1,001–1,250	0.003	Wet
Coleoptera	1,501–1,750	0.01	Wet
Hemiptera	1,501–1,750	< 0.001	Dry
Hemiptera	1,751–1,830	0.057	Dry
Formicidae	751–1,000	0.03	Dry
Formicidae	1,501–1,750	0.02	Wet
Lepidoptera	1,501–1,750	< 0.001	Wet

A similar lack of concentration on one or two categories of prey appeared in a series of ten stomachs from Kenya frogs (LOVERIDGE, 1936). *Diptera* were present in five stomachs, *Lepidoptera* and *Coleoptera* in three, *Formicidae* and *Diplopoda* in two, and *Hemiptera*, *Orthoptera*, and *Neuroptera* in one.

TABLE 24. — **Statistically significant altitudinal variation in volumes of given prey eaten by *Rana fuscigula* in the Parc National de l'Upemba.**

Prey	Season	P	Altitudes of maximum consumption
Lepidoptera	Wet	< 0.001	1,501–1,750
Formicidae	Dry	< 0.001	585– 750
Hemiptera	Dry	0.01	1.751–1,830
Araneida	Dry	0.02	1,251–1,500

In only three season-altitude zones did the diet of *fuscigula* depart significantly from uniformity (Table 22). In those zones *Coleoptera*, *Araneida*, *Lepidoptera*, *Hemiptera*, *Orthoptera*, and *Formicidae* were eaten in larger volumes, in roughly that order.

Seasonal variation in the diet (Table 23) followed availability at least in the case of *Mollusca*, which were consistently eaten in larger volumes in the wet season. Gastropods are known to be more active in the wet season and, hence, more exposed to predation then. They appeared in only 7 (6 %) dry season stomachs but in 31 (21 %) wet season stomachs. The relation of seasonal abundance of the other prey types to predation by *Rana fuscigula* is uncertain.

A moderate amount of altitudinal variation in diet was found (Table 24). The greater consumption of *Formicidae* below 1,000 m is a pattern evident also in the diet of *Phrynobatrachus* (p. 66).

The average volume of individual food organisms within 50 stomachs chosen at random varied from 0.001 to 0.80 ml (median 0.073). The total volume of food within these stomachs varied from 0.001 (1 item) to 2.34 ml (7 items). Thirteen stomachs each contained one item, ten contained 2, six 3, nine 4, six 5, one 6, one 7, one 9, two 15, and one 23.

Snout-vent lengths in the 50 frogs from which these stomachs were taken ranged from 40.8 to 97.5 mm (median 56.8). Correlation between snout-vent and average volume of individual prey was +0.187 (Spearman rank coefficient), which is not statistically significant ($P = 0.09$).

Rana frontalis.

Sixty-seven stomachs with food were examined, 58 of them from the wet season. All are from 585-750 m.

TABLE 25. — **Taxonomic distribution of prey found in 67 stomachs of** *Rana frontalis* **from the Parc National de l'Upemba.**

Number of stomachs containing principal groups given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.
Araneida (22).

Chilopoda. — *Geophilomorpha.*

Insecta.
Odonata. — *Anisoptera* (1).
Blattaria (16).
Orthoptera (37).
Acrididae.
Gryllidae.
Tetrigidae.
Tettigoniidae.
Dermaptera.
Isoptera. — *Termitidae* (9).
Hemiptera (7).
Homoptera.
Jassidae.
Reduviidae.
Lepidoptera (4).
Diptera (3).
Asilidae.
Tipulidae.
Coleoptera (11).
Curculionidae.
Elateridae.
Scarabaeidae.
Hymenoptera.
Formicidae (8).

CHORDATA. — **Amphibia** (1).

The taxonomic composition of the diet is given in Table 25. The prey consisted mostly of large, active, terrestrial invertebrates. With the exception of one *Odonata*, one tipulid, and one newly metamorphosed frog, none of the prey could even be considered semiaquatic. *Isoptera* were usually eaten after flights; 5 of the 8 wet season stomachs containing *Isoptera* held only imagos.

The various prey categories were not eaten in equal volumes during the wet season ($P < 0.001$); the three principal food categories were *Orthoptera*, *Araneida*, and *Blattaria*. The food did not depart significantly ($P = 0.25$) from homogeneity during the dry season, though the three principal categories were exactly as in the wet season.

No seasonal changes in the volumes of given food categories were detected; in each test of these differences P exceeded 0.20.

The average volume of food organisms in 50 stomachs chosen at random varied from 0.001 to 0.300 ml (median 0.097). The total volumes within stomachs varied from 0.001 (1 item) to 0.59 ml (6 items). Twenty-two stomachs contained a single item, ten contained 2 items, twelve 3 to 5, and four 6 to 8.

Snout-vent lengths of the 50 frogs from which these stomachs were taken ranged between 35.0 and 46.7 mm (median 41.9 mm). The Spearman rank correlation between snout-vent and average volume of individual prey within stomachs was +0.40, which is statistically significant ($P = 0.006$).

Rana mascareniensis.

One hundred food containing stomachs were examined. All were from frogs collected at 585-750 m, 75 of them in the wet season.

Taxonomic composition of the diet is given in Table 26. Although most of the prey are terrestrial organisms (e.g., all of the *Coleoptera* and *Orthoptera*), many stomachs contained aquatic or semiaquatic organisms. Two of the *Odonata* eaten were nymphs; the adults may be considered semiaquatic. The aquatic *Hemiptera*, *Hydrometridae* and *Gerridae*, occurred in four stomachs. The *Amphibia* eaten comprised tadpoles in four stomachs and newly metamorphosed juveniles (probably caught at the margins of bodies of water) in the remaining seven. Of the *Isoptera* eaten, all but those in one stomach were imagos, indicating that they were eaten following nuptial flights.

TABLE 26.

Taxonomic composition of food found in 100 stomachs of *Rana mascareniensis* **from the Parc National de l'Upemba.**

Number of stomachs containing principal groups given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

- **Crustacea.** — *Isopoda.*
- **Arachnida.**
  - *Araneida* (35).
- **Insecta.**
  - *Odonata* (12).
  - *Blattaria* (5).
  - *Orthoptera* (22).
    - *Acrididae.*
    - *Gryllidae.*
    - *Phasmatidae.*
    - *Tetrigidae.*
    - *Tettigoniidae.*
  - *Dermaptera.*
  - *Isoptera* (6).
  - *Hemiptera* (29).
    - *Cercopidae.*
    - *Cicadellidae.*
    - *Gerridae.*
    - *Hydrometridae.*
    - *Jassidae.*
    - *Lygaeidae.*
    - *Nerthridae.*
    - *Pentatomidae.*
    - *Reduviidae.*
  - *Lepidoptera* (12).
  - *Diptera* (5).
    - *Diopsidae.*
    - *Syrphidae.*
  - *Coleoptera* (38).
    - *Carabidae.*
    - *Chrysomelidae.*
    - *Cicindelidae.*
    - *Curculionidae.*
    - *Elateridae.*
    - *Lagriidae.*
    - *Scarabaeidae.*
    - *Staphylinidae.*
    - *Tenebrionidae.*
  - *Hymenoptera.*
    - *Apidae.*
    - *Formicidae* (16).

CHORDATA. — **Amphibia** (11).

In nine stomachs removed from Kenya specimens, LOVERIDGE (1936) found *Orthoptera* in five, *Araneida* in three, *Lepidoptera* in two, and *Formicidae*, *Blattaria*, *Diptera*, and *Coleoptera* in one each.

The diet diverged from homogeneity to a significant extent (P = 0.004) in the wet season, at which time *Coleoptera*, *Araneida*, and *Hemiptera* were the three main groups eaten. The groups eaten in greatest amounts in the dry season were *Araneida*, *Odonata*, and *Hemiptera*, though the departure from homogeneity was not significant (P = 0.35).

No significant seasonal variation in the volumes of a given prey category was found. In every group tested, P was greater than 0.30.

Average volume of individual food organisms in 50 stomachs chosen at random ranged between 0.010 and 0.840 ml (median 0.060). The total volumes within stomachs varied from 0.02 (1 item) to 0.84 ml (1 item). Eighteen stomachs contained one item, fifteen contained 2, eleven 3 to 5, five 7 to 10, and one 12.

Snout-vent lengths of these 50 frogs varied from 36.9 to 56.9 mm (median 43.2). The Spearman rank correlation between snout-vent and average volume of individual prey within stomachs was +0.072, which is not significant (P = 0.6).

Rana grandisonae.

The 106 food-containing stomachs examined had the following distribution.

Meters	751-1,000	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	2	—	35	34
Dry season	—	11	—	24

The taxonomic composition of the diet is given in Table 27. Active terrestrial arthropods dominated the diet, though semiaquatic or aquatic organisms were also eaten. Aquatic *Coleoptera* occurred in five stomachs, *Dytiscidae* larvae in four and *Hydrophilidae* in one. The amphibians eaten were small; about one half were under 11 mm.

Only in the wet season at 1,751-1,830 m did the diet depart from homogeneity to a statistically significant extent (P = 0.03). In that season and altitude, *Orthoptera*, *Araneida*, and *Coleoptera* were the three principal food categories, closely followed by *Amphibia*. In the other seasonal-altitudinal zones deviation from homogeneity was not significant (P = 0.2-0.8). *Araneida*, *Orthoptera*, and *Coleoptera* were eaten in the largest volumes.

Seasonal variation, which could only be tested at 1,751-1,830 m, appeared just in *Orthoptera* (P=0.012); larger volumes were eaten in the wet season. Differences between wet and dry seasons in amounts of *Araneidae*, *Coleoptera*, and *Amphibia* were not significant (P = 0.31-0.54).

TABLE 27.

Taxonomic distribution of prey found in 106 stomachs of *Rana grandisonae* from the Parc National de l'Upemba.

Numbers of stomachs containing principal food categories given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

- **Crustacea.** — *Isopoda.*
- **Arachnida.**
  - *Araneida* (39).
  - *Phalangida.*
- **Chilopoda.** — *Geophilomorpha.*
- **Diplopoda.**
- **Insecta.**
  - *Odonata* (4).
    - *Zygoptera.*
  - *Blattaria* (9).
  - *Orthoptera* (38).
    - *Acrididae.*
    - *Gryllidae.*
    - *Manteidae.*
    - *Tetrigidae.*
    - *Tettigoniidae.*
  - *Dermaptera.*
  - *Isoptera.* — *Termitidae.*
  - *Hemiptera* (20).
    - *Cicadellidae.*
    - *Fulgoridae.*
    - *Lygaeidae.*
    - *Pentatomidae.*
    - *Reduviidae.*
  - *Lepidoptera* (15).
  - *Diptera* (8).
  - *Coleoptera* (33).
    - *Anthicidae.*
    - *Cerambycidae.*
    - *Chrysomelidae.*
    - *Cistelidae.*
    - *Curculionidae.*
    - *Dytiscidae.*
    - *Elateridae.*
    - *Erotylidae.*
    - *Hydrophilidae.*
    - *Lagriidae.*
    - *Scarabaeidae.*
    - *Staphylinidae.*
  - *Hymenoptera.*
    - *Formicidae* (5).
    - *Ichneumonidae.*
    - *Tenthredinidae.*
    - *Vespidae.*

CHORDATA. — **Amphibia** (21).

Tests of altitudinal variation were limited to the 1,251-1,500 and 1,751-1,830 m zones during dry season and the 1,501-1,750 and 1,751-1,830 m zones during the wet season. *Coleoptera* were eaten in greater amounts at 1,751-1,830 m during the dry season ($P < 0.001$). No other statistically significant altitudinal differences were found in *Orthoptera*, *Araneida*, and *Amphibia* ($P = 0.26$-0.76).

The average volume of individual prey within 50 stomachs chosen at random varied from 0.018 to 0.300 ml (median 0.052). The total volume of prey in these stomachs varied between 0.02 (1 item) and 0.78 ml (3 items). Twelve stomachs contained one item each, sixteen contained 2, fourteen 3, seven 4 to 6, and one 11.

The frogs from which these 50 stomachs were taken had snout-vent lengths of 34.2-49.4 mm (median 39.2). The Spearman rank correlation coefficient between these snout-vent lengths and average volume of individual prey within stomachs was +0.294, a statistically significant value ($P = 0.02$).

Rana uzungwensis.

The 42 stomachs examined had the following distribution:

Meters	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	2	5	8	3	12
Dry season	1	—	11	—	—

Taxonomic composition of the diet is given in Table 28. With the exception of one adult *Odonata* and one juvenile frog, all organisms are terrestrial invertebrates.

Tests of the uniformity of diet were carried out for the 1,251-1,500 m zone at both seasons and for the 1,751-1,830 zone at the wet season. In no case was the departure from homogeneity significant (P between 0.3 and 0.8). The food classes eaten in greatest volumes were, as suggested by the numbers in Table 28, *Lepidoptera*, *Orthoptera*, and *Araneida*.

TABLE 28.

Taxonomic composition of prey found in 42 stomachs of *Rana uzungwensis* **from the Parc National de l'Upemba.**

Number of stomachs containing principal food categories given in parentheses.

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Arachnida.

- *Araneida* (12).
- *Phalangida.*

Insecta.

- *Odonata.*
- *Blattaria* (6).
- *Orthoptera* (12).
  - *Acrididae.*
  - *Gryllidae.*
  - *Phasmatidae.*
  - *Tetrigidae.*
- *Dermaptera.*
- *Hemiptera* (5).
  - *Cicadellidae.*
  - *Pentatomidae.*
  - *Reduviidae.*
- *Lepidoptera* (12).
- *Coleoptera* (8).
  - *Carabidae.*
  - *Chrysomelidae.*
  - *Elateridae.*
  - *Histeridae.*
  - *Scarabaeidae.*
  - *Staphylinidae.*
- *Hymenoptera.*
  - *Apoidea.*
  - *Formicidae* (4).

CHORDATA. — **Amphibia** (1).

The numbers available did not make tests of seasonal or altitudinal variation worth while.

Average volume within stomachs of individual prey varied from 0.008 to 0.45 ml (median 0.050). The total volume within stomachs ranged between 0.02 (1 item) and 0.90 ml (2 items). Sixteen stomachs each contained a single prey organism, thirteen contained 2, nine 3, one 4, one 5, and one 8.

Snout-vent lengths of the 42 frogs from which these stomachs were taken had a range of 31.4-45.7 mm (median 35.3). The Spearman rank correlation coefficient between snout-vent and average volume individual prey within stomachs was +0.250 ($P = 0.05$).

Rana porosissima.

The 132 stomachs examined had the following distribution :

Meters	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	—	41	42
Dry season	10	18	21

Taxonomic composition of the diet is given in Table 29. With the exception of 9 juvenile frogs, all of the prey consisted of terrestrial invertebrates, most of them very active forms (e.g., *Orthoptera*, *Blattaria*, and *Araneida*). At no season or altitude, did the diet depart significantly from

TABLE 29. — **Taxonomic distribution of prey found in 132 stomachs of** *Rana porosissima* **from the Parc National de l'Upemba.**

Numbers of stomachs containing principal groups given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

- **Crustacea.** — *Isopoda.*
- **Arachnida.**
  - *Araneida* (27).
  - *Phalangida.*
- **Chilopoda.** — *Geophilomorpha.*
- **Diplopoda.**
- **Insecta.**
  - *Blattaria* (20).
  - *Orthoptera* (34).
    - *Acrididae.*
    - *Gryllidae.*
    - *Manteidae.*
    - *Mogoplistidae.*
    - *Phasmatidae.*
    - *Tetrigidae.*
    - *Tettigoniidae.*
  - *Dermaptera.*
  - *Isoptera.* — *Termitidae.*
  - *Hemiptera* (16).
    - *Fulgoridae.*
    - *Homoptera.*
    - *Jassidae.*
    - *Lygaeidae.*
    - *Pentatomidae.*
    - *Reduviidae.*
  - *Lepidoptera* (33).
  - *Diptera* (12).
    - *Diopsidae.*
    - *Syrphidae.*
    - *Tipulidae.*
  - *Coleoptera* (30).
    - *Carabidae.*
    - *Cerambycidae.*
    - *Chrysomelidae.*
    - *Curculionidae.*
    - *Elateridae.*
    - *Lagriidae.*
    - *Lampyridae.*
    - *Scarabaeidae.*
    - *Staphylinidae.*
    - *Tenebrionidae.*
  - *Hymenoptera.*
    - *Braconidae.*
    - *Formicidae* (23).
    - *Ichneumonidae.*

CHORDATA. — **Amphibia** (9).

TABLE 30. — **Test of uniformity of diet of *Rana porosissima* from the Parc National de l'Upemba.**

Altitude	Season	P	Principal food categories
1,251-1,500	Dry	0.86	*Araneida, Blattaria, Lepidoptera*
1,501-1,750	Wet	0.08	*Lepidoptera, Orthoptera, Araneida*
1,501-1,750	Dry	0.42	*Formicidae, Coleoptera, Lepidoptera*
1,751-1,830	Wet	0.31	*Orthoptera, Lepidoptera, Coleoptera*
1,751-1,830	Dry	0.74	*Orthoptera, Araneida, Formicidae*

homogeneity (Table 30). No two or three food categories can be designated as dominant. *Rana porosissima* feeds almost at random among the most abundant, active, terrestrial arthropods.

Minor seasonal changes appeared in the volumes of particular prey eaten (Table 31). No pattern emerges from these changes. No significant altitudinal variation was found.

The average volume of individual food organisms in 50 stomachs chosen at random varied from 0.001 to 0.500 ml (median 0.052). The total volumes within stomachs varied between 0.001 (1 item) and 0.68 ml (2 items). Twenty stomachs each contained one item, twelve 2, eleven 3 to 4, six 6 to 7, and one 10.

TABLE 31. — **Statistically significant seasonal variation in volumes of prey eaten by *Rana porosissima* in the Parc National de l'Upemba.**

Prey	Altitude	P	Season of greater consumption
Orthoptera	1,501-1,750	0.05	Dry
Blattaria	1,501-1,750	0.03	Wet
Blattaria	1,751-1,830	0.02	Wet
Lepidoptera	1,501-1,750	0.003	Dry
Lepidoptera	1,751-1,830	0.02	Wet
Hemiptera	1,501-1,750	0.046	Wet
Araneida	1,751-1,830	0.04	Dry

Snout-vent lengths of the frogs from which these stomachs came varied between 31.2 and 52.7 mm (median 40.4). The correlation between snout-vent lengths of the frogs and average volumes of the individual prey each contained was insignificant (Spearman rank coefficient +0.031; P = 0.9).

SUMMARY OF RANA (PTYCHADENA) SPECIES.

Although few instances of statistically significant deviations from uniformity appeared (Table 32), the diets of this group of species consist primarily of large, active, terrestrial invertebrates : *Orthoptera*, *Araneida*, and *Coleoptera*. The relative insignificance of *Formicidae* in all of these diets indicates that simple availability in terms of numbers of individuals

TABLE 32. — **Statistically significant deviations from uniformity in diets of species of *Rana* (*Ptychadena*) from the Parc National de l'Upemba.**

Species	Altitude	Season	Dominant food
frontalis	585– 750	Wet	*Orthoptera, Araneida, Blattaria*
mascareniensis	585– 750	Wet	*Coleoptera, Araneida, Hemiptera*
grandisonae	1,751–1,830	Wet	*Orthoptera, Araneida, Coleoptera*

is not the explanation for the dominance of the prey categories in Table 32, though *Araneida* and *Coleoptera* are among the most abundant terrestrial invertebrates. Probably *Formicidae* are below the normal size range of prey of adult of these species (see Table 71 and the discussion on p. 80), and so are eaten less often.

Seasonal variation in diet was extensive only in *porosissima* (Table 31). Even within that species, however, the seasonal changes do not fall into a pattern : *Lepidoptera* were eaten in greater amounts during the wet season at one elevation and during the dry season at a different altitude; *Blattaria* were eaten in greater amounts during the wet season at both altitudes; the other categories show seasonal change only in one altitudinal zone or the other. *Rana grandisonae* ate more *Orthoptera* during the wet season at one altitudinal zone. Otherwise *grandisonae* and the other three species showed no seasonal variation.

Because of the narrow altitudinal distributions of these species (SCHMIDT and INGER, 1959), this type of variation in diet could not be tested in two of the five species. Of the three that range through a number of altitudinal zones, only *grandisonae* showed significant altitudinal changes in diet, and those were limited to one type of prey (*Coleoptera*) during the dry season.

Rana frontalis ate more *Orthoptera* than *mascareniensis* in both seasons in the lowest altitudes whereas *mascareniensis* ate more *Coleoptera*, *Hemiptera*, and aquatic or semiaquatic food (Table 33). Differences among the high altitude species were not as consistent (Table 33). Significant differences in amounts of aquatic food eaten may result from differences in habitat preferences that, in turn, affect availability.

TABLE 33. — **Significant differences among species of *Rana* (*Ptychadena*) in amounts of given prey eaten in the Parc National de l'Upemba.**

Prey	Altitude	Season	P	Species compared, in order of decreasing consumption
Orthoptera	585– 750	Wet	< 0.001	*frontalis, mascareniensis*
Hemiptera	585– 750	Wet	0.028	*mascareniensis, frontalis*
Coleoptera	585– 750	Wet	0.002	*mascareniensis, frontalis*
Aquatic (*)	585– 750	Wet	0.006	*mascareniensis, frontalis*
Orthoptera	585– 750	Dry	0.006	*frontalis, mascareniensis*
Lepidoptera	1,501–1,750	Wet	< 0.001	*porosissima, grandisonae*
Araneida	1,751–1,830	Wet	0.04	*grandisonae, uzungwensis, porosissima*
Aquatic (*)	1,751–1,830	Wet	< 0.001	*grandisonae, uzungwensis, porosissima*
Coleoptera	1,751–1,830	Dry	0.048	*grandisonae, porosissima*

The size of the prey of these five species does not differ significantly. The Kruskal-Wallis test applied to the 50 stomachs of each (41 of *uzungwensis*) chosen at random shows that the null hypothesis must be accepted ($H = 7.58$; $P = 0.11$).

The average volume of individual prey within stomachs is correlated with the snout-vent lengths of the frogs in *frontalis* (+0.40), *grandisonae* (+0.29), and *uzungwensis* (+0.25), although the coefficients are not large. As Table 71 shows, the five species are so similar in size that a test of correlation between species is not warranted. These five species are also alike in the number of prey found in each stomach; the median values are identical and the maxima are closely grouped.

(*) Aquatic or semiaquatic organisms, comprising young frogs or tadpoles, *Odonata*, *Dytiscidae*, *Hydrophilidae*, *Gerridae* and *Hydrometridae*.

Genus **ARTHROLEPTIS** Smith.

Arthroleptis stenodactylus.

Food containing stomachs of 215 frogs were examined. The frogs had the following distribution :

Meters	585-750	751-1,000	1,001-1,250	1,501-1,500	1,751-1,830
Wet season	108	43	31	22	1
Dry season	4	1	—	5	—

The taxonomic distribution of the food is given in Table 34. That none of the prey categories is aquatic was to be expected as *stenodactylus* does not visit aquatic habitats even to breed.

The numbers of stomachs in which given types of prey occurred are roughly parallel to their importance in terms of volumes eaten (Table 35). *Isoptera* and *Formicidae* clearly dominated the diet except in the 1,251-1,500 m zone where no deviation from uniformity is indicated. *Coleoptera*, *Orthoptera*, and *Chilopoda* formed a second echelon of important prey, though at a much lower level than *Isoptera* and *Formicidae*.

At the two lowest altitudinal zones, a larger proportion of the *Isoptera* eaten were imagoes than neuter castes, suggesting that most termites were eaten at those elevations after nuptial flights. The reverse was true in the 1,001-1,250 m zone where a larger volume of workers and soldiers were eaten. Applying the Mann-Whitney U test, the hypothesis of no difference between volumes of imagoes and neuters eaten was rejected at the $P = 0.001$ level in all three zones. Too few stomachs from the 1,251-1,500 m zone contained *Isoptera* to make a test worthwhile.

The majority of stomachs from the 585-750 m zone were from frogs caught in December, January, and February; those from the 751-1,000 m zone were caught in November. But most of those from the 1,001-1,250 m zone were from frogs caught in March, near the end of the wet season. If the frequency of termite flights is reduced towards the close of the rainy season, the change in emphasis from imago to neuter *Isoptera* may be explained partly on the basis of the portion of rainy season from which the frogs came. One of the weaknesses of this report is the lumping of all months of the wet season and the possible obscuring of changes within each season.

The few specimens available from the dry season preclude test of seasonal differences. Altitudinal differences in volumes eaten were found in *Isoptera* and *Annelida*. The greatest volume of *Isoptera* was eaten in the 751-1,000 m zone, followed in order by the volumes in the 1,001-1,250, 585-750, and 1,251-1,500 m zones; the hypothesis of no difference among zones was rejected at the $P = 0.035$ level. *Annelida* were eaten in greatest volume in

TABLE 34.

Taxonomic distribution of prey in 215 stomachs of *Arthroleptis stenodactylus* from the Parc National de l'Upemba.

Number of stomachs containing principal food types given in parentheses.

ANNELIDA. — **Oligochaeta** (25).

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

- **Crustacea.** — *Isopoda* (17).
- **Arachnida.**
  - *Acarina.*
  - *Araneida* (27).
  - *Phalangida.*
- **Diplopoda.**
- **Chilopoda.** — *Geophilomorpha* (20).
- **Insecta.**
  - *Thysanura.*
  - *Collembola.*
  - *Blattaria* (18).
  - *Orthoptera* (37).
    - *Acrididae.*
    - *Gryllidae.*
    - *Gryllotalpidae.*
    - *Tetrigidae.*
    - *Tettigoniidae.*
  - *Dermaptea.*
  - *Isoptera.* — *Termitidae* (90).
  - *Hemiptera* (18).
    - *Aradidae.*
    - *Cicadellidae.*
    - *Cydnidae.*
    - *Henicocephalidae.*
    - *Jassidae.*
    - *Lygaeidae.*
    - *Membracidae.*
    - *Reduviidae.*
    - *Tingidae.*
  - *Lepidoptera* (21).
  - *Diptera* (15).
    - *Chironomidae.*
    - *Nematocera.*
    - *Stratiomyidae.*
    - *Tabanidae.*
    - *Tipulidae.*
  - *Coleoptera* (50).
    - *Anthicidae.*
    - *Brenthidae.*
    - *Buprestidae.*
    - *Carabidae.*
    - *Cerambycidae.*
    - *Chrysomelidae.*
    - *Coccinellidae.*
    - *Curculionidae.*
    - *Elateridae.*
    - *Histeridae.*
    - *Nitidulidae.*
    - *Scarabaeidae.*
    - *Staphylinidae.*
    - *Tenebrionidae.*
  - *Hymenoptera.*
    - *Chalcidoidea.*
    - *Formicidae* (110).

CHORDATA. — **Amphibia** (1).

the 1,251-1,500 m zone, followed by the volumes of the 585-750, 751-1,000, and 1,001-1,250 m zones; the hypothesis of no difference among zones was rejected at the $P = 0.001$ level. *Formicidae*, *Coleoptera*, and *Orthoptera* were eaten in approximately equal volumes at all elevations.

The average volume of individual prey within each of 50 stomachs chosen at random varied from 0.001 to 0.42 ml (median 0.012). Total volume of food in these 50 varied from 0.004 (3 items) to 0.81 ml (12 items), and the number of prey items from 1 to 66. Nine stomachs contained one item, twelve 2 or 3, seven 4 to 6, eight 7 to 10, seven 11 to 20, three 21 to 30, and four 37 to 66.

Snout-vent lengths of the 50 frogs from which these stomachs came ranged from 16.9 to 36.0 mm (median 28.3). The Spearman rank correlation between snout-vent length and average volume of individual prey is +0.236. This coefficient is statistically significant, corresponding to $P = 0.05$ ($t = 1.68$).

TABLE 35. — **Test of uniformity of diet of *Arthroleptis stenodactylus* from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	*< 0.001*	*Formicidae, Isoptera, Orthoptera*
751–1,000	Wet	*< 0.001*	*Isoptera, Formicidae, Chilopoda*
1,001–1,250	Wet	*< 0.001*	*Isoptera, Formicidae, Coleoptera*
1,251–1,500	Wet	0.60	*Annelida, Formicidae, Orthoptera*

Genus **PHRYNOBATRACHUS** Günther.

Phrynobatrachus anotis.

Individuals containing fresh food were collected only at elevations above 1,500 m. The stomachs analyzed had the following distribution :

Meters	1,501-1,750	1,751-1,830
Wet season	11	62
Dry season	36	12

The taxonomic composition of the diet is given in Table 36.

Coleoptera, *Formicidae*, and *Araneida* dominated the diet, which consisted entirely of terrestrial invertebrates. Statistically significant differences in the amounts eaten of each prey type were found in the dry season at the 1,501-1,750 m zone and in the wet season at the highest altitudinal zone (Table 37).

Seasonal differences in the diet were statistically significant only in the 1,751-1,830 m zone (Table 38). Greater volumes of *Coleoptera* were eaten during the dry season, and larger volumes of ants eaten during the wet season. Altitudinal variation in the diet involved only ants (Table 39).

In 50 frogs chosen at random, the average volume of the prey ranged from 0.001 to 0.057 ml (median 0.0032 ml). Total prey volume in these stomachs varied from 0.001 (1 item) to 0.172 ml (12 items). Only 5 stomachs held more than 9 items, the maximum being 16. Snout-vent lengths of these 50 frogs were 15.7-23.3 mm (median 19.9 mm). The average volume within stomachs of individual prey was not correlated with the size of the frog (Spearman rank correlation = −0.08).

TABLE 36.

Taxonomic distribution of food found in 115 stomachs of *Phrynobatrachus anotis* from the Parc National de l'Upemba.

Number of stomachs in which nine principal groups occurred given in parentheses.

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.

Acarina.
Araneida (36).

Chilopoda.

Scolopendridae.

Insecta.

Collembola.
Entomobryidae.
Sminthuridae.
Blattaria (11).
Orthoptera (6).
Gryllidae.
Tetrigidae.
Isoptera (4).
Termitidae.
Thysanoptera.
Ideothripidae.
Phloeothripidae.
Hemiptera (36).
Aphididae.
Areopodidae.
Cicadellidae.
Fulgoridae.
Hebridae.
Miridae.
Pentatomidae.
Pleidae.
Pyrrhocoridae.
Reduviidae.
Tingidae.
Veliidae.
Trichoptera.
Hydroptilidae.
Lepidoptera (14).
Geometridae.
Diptera (33).
Anthomyidae.
Asilidae.
Bibionidae.
Calliphoridae.
Chironomidae.
Clusiidae.
Culicidae.
Dolichopodidae.
Leptoceridae.
Muscidae.
Mycetophilidae.
Phoridae.
Phryneidae.
Piophilidae.
Scopeumatidae.
Syrphidae.
Tabanidae.
Tipulidae.
Trypetidae.
Coleoptera (59).
Anobiidae.
Anthicidae.
Buprestidae.
Carabidae.
Chrysomelidae.
Cupidae.
Curculionidae.
Cyphonidae.
Elateridae.
Helodidae.
Nitidulidae.
Pselaphidae.
Ptinidae.
Scarabaeidae.
Staphylinidae.
Tenebrionidae.
Throscidae.
Hymenoptera.
Agaonidae.
Braconidae.
Eurytomidae.
Formicidae (50).
Ichneumonidae.
Perilampidae.
Platygasteridae.
Sphecidae.

TABLE 37. — **Test of uniformity of diet of** *Phrynobatrachus anotis* **from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
1,501-1,750	Wet	0.13	*Lepidoptera, Coleoptera, Formicidae*
1,501-1,750	Dry	*0.001*	*Formicidae, Coleoptera, Diptera*
1,751-1,830	Wet	*0.001*	*Coleoptera, Araneida, Formicidae*
1,751-1,830	Dry	0.07	*Coleoptera, Hemiptera, Araneida*

TABLE 38.

Seasonal variation in volume of given prey eaten by *Phrynobatrachus anotis* **in the Parc National de l'Upemba.**

Probabilities for significant variations given in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	1,501-1,750	0.51	Wet
Formicidae	1,751-1,830	*0.017*	Wet
Coleoptera	1,501-1,750	0.16	Wet
Coleoptera	1,751-1,830	*0.001*	Dry
Hemiptera	1,501-1,750	0.75	Dry
Hemiptera	1,751-1,830	0.21	Wet
Diptera	1,501-1,750	0.29	Dry
Diptera	1,751-1,830	0.31	Wet

Significant deviation from uniformity in the diet was found only in the wet season at the lowest elevation, in the wet season at the 1,501-1,750 m zone, and in both seasons at the 1,751-1,830 m zone (Table 41). *Coleoptera*, *Hemiptera*, and *Formicidae* were the most important prey. *Isoptera* were not eaten in large quantities even at the lowest elevation.

Seasonal variation (Table 42) could be tested only for the two highest altitudinal zones because of the distribution of stomachs available (see

TABLE 39.

Altitudinal variation in volume of given prey eaten by *Phrynobatrachus anotis* in the Parc National de l'Upemba.

Probabilities for significant variations given in italics.

Prey	Season	P	Altitude of greater consumption
Formicidae	Wet	0.74	1,751-1,830
Formicidae	Dry	*0.008*	1,501-1,750
Coleoptera	Wet	0.48	1,501-1,750
Coleoptera	Dry	0.056	1,751-1,830
Hemiptera	Wet	0.82	1,751-1,830
Hemiptera	Dry	0.77	1,751-1,830
Diptera	Wet	0.44	1,751-1,830
Diptera	Dry	0.17	1,501-1,750

tabulation above). Seasonal changes were evident only in the volumes of *Formicidae* and *Coleoptera*, which were eaten in larger quantities in the wet season.

Significant altitudinal variation in volumes eaten was found in each of the four most important prey types (Table 43). Because of the distribution of stomachs only four altitudinal zones could be used for each season. Only *Formicidae* were eaten in larger volumes at the lower elevations.

The average volume of food organisms in 50 stomachs chosen at random varied from 0.0005 to 0.040 ml (median 0.0022). In these 50 stomachs the total volume of food ranged from 0.0009 (2 items) to 0.106 ml (3 items).

Phrynobatrachus cryptotis.

The 270 stomachs examined had the following distribution :

Meters … … …	585-750	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season . … …	85	—	8	—	47	40
Dry season . … …	—	15	—	23	8	44

The taxonomic composition of the diet is given in Table 40. The only aquatic organisms found were an *Odonata* nymph (in one stomach), *Gerridae* (two stomachs), *Hydrophilidae* (two stomachs), and *Dytiscidae* (one stomach).

TABLE 40. — **Taxonomic distribution of food occurring in 270 stomachs of *Phrynobatrachus cryptotis* collected in the Parc National de l'Upemba.**

Number of stomachs in which nine principal groups occurred given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.

Acarina.
Araneida (54).

Chilopoda.

Scolopendridae.

Insecta.

Thysanura. — *Lepismatidae.*

Collembola.
Entomobryidae.
Sminthuridae.

Odonata.

Blattaria (10).

Orthoptera (11).
Gryllidae.
Tetrigidae.

Isoptera (25).
Termitidae.

Thysanoptera.
Phloeothripidae.

Hemiptera (73).
Aphididae.
Cicadellidae.
Corizidae.
Fulgoridae.
Gerridae.
Lygaeidae.
Miridae.
Nabidae.
Pentatomidae.
Reduviidae.
Tingidae.
Veliidae.

Lepidoptera (9).
Phalaenidae.

Diptera (47).
Bibionidae.
Chironomidae.
Chloropidae.
Culicidae.
Dolichopodidae.
Drosophilidae.
Empididae.
Heleidae.
Phoridae.
Phryneidae.
Piophilidae.
Pipunculidae.
Psychodidae.
Rhyphidae.
Sarcophagidae.
Syrphidae.
Tabanidae.
Tachinidae.
Tipulidae.
Trypetidae.

Coleoptera (87).
Anthicidae.
Bostrychidae.
Buprestidae.
Carabidae.
Cerambycidae.
Chrysomelidae.
Coccinellidae.
Curculionidae.
Cybocephalidae.
Dermestidae.
Dytiscidae.
Elateridae.
Helodidae.
Histeridae.
Hydrophilidae.
Languriidae.
Lathridiidae.
Melasidae.
Mordellidae.
Orthoperidae.
Phalacridae.
Pselaphidae.
Scarabaeidae.
Staphylinidae.
Tenebrionidae.
Throscidae.

Hymenoptera.
Apidae.
Braconidae.
Eulophidae.
Eurytomidae.

Formicidae (138).
Ichneumonidae.
Mymaridae.
Perilampidae.
Platygasteridae.
Pteromalidae.
Vespidae.
Xiphydriidae.

TABLE 41. — **Test of uniformity of diet of *Phrynobatrachus cryptotis* from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	< *0.001*	*Formicidae, Araneida, Coleoptera*
751–1,000	Dry	0.8	*Diptera, Isoptera, Formicidae*
1,001–1,250	Wet	0.28	*Formicidae, Orthoptera, Diptera*
1,251–1,500	Dry	0.25	*Araneida, Formicidae, Coleoptera*
1,501–1,750	Wet	< *0.001*	*Hemiptera, Coleoptera, Formicidae*
1,501–1,750	Dry	0.56	*Hemiptera, Coleoptera, Araneida*
1,751–1,830	Wet	< *0.001*	*Coleoptera, Formicidae, Hemiptera*
1,751–1,830	Dry	< *0.001*	*Hemiptera, Coleoptera, Diptera*

TABLE 42.

Seasonal variation in volume of given prey eaten by *Phrynobatrachus cryptotis* in the Parc National de l'Upemba.

Probabilities for significant variations given in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	1,501–1,750	< *0.001*	Wet
Formicidae	1,751–1,830	*0.002*	Wet
Coleoptera	1,501–1,750	0.96	Wet
Coleoptera	1,751–1,830	*0.016*	Wet
Hemiptera	1,501–1,750	0.42	Wet
Hemiptera	1,751–1,830	0.21	Dry
Diptera	1,501–1,750	0.90	Wet
Diptera	1,751–1,830	0.57	Wet
Isoptera	1,751–1,830	0.20	Wet

TABLE 43.

Altitudinal variation in volume of given prey eaten by *Phrynobatrachus cryptotis* in the Parc National de l'Upemba.

Probabilities for significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	< *0.001*	585– 750
Formicidae	Dry	0.11	1,251–1,500
Coleoptera	Wet	< *0.001*	1,751–1,830
Coleoptera	Dry	0.12	1,501–1,750
Hemiptera	Wet	< *0.001*	1,501–1,750
Hemiptera	Dry	*0.014*	1,751–1,830
Diptera	Wet	*0.01*	1,001–1,250
Diptera	Dry	0.33	751–1,000
Isoptera	Wet	0.08	585– 750

Two stomachs contained the minimal-sized prey; one held 2 items and the other 3. The largest prey was the only item in that particular stomach. Eight stomachs contained one item, ten 2, fifteen 3 to 5, seven 6 to 10, nine 11 to 20, and one 25.

Snout-vent lengths of the 50 frogs ranged from 15.1 to 21.0 mm (median 17.4 mm) and bore no statistically significant relation to the average volume within stomachs of individual prey (Spearman correlation coefficient = -0.168).

Phrynobatrachus perpalmatus.

This species was collected only in the lowest altitudinal zone (585-750 m). The contents of 91 wet season and 28 dry season stomachs were analyzed. The taxonomic composition of the diet is given in Table 44.

Although *perpalmatus* is more aquatic than the other species of *Phrynobatrachus* studied, its diet consisted mostly of terrestrial animals. The aquatic groups eaten were : *Odonata* (in 2 stomachs), *Gerridae* (3), *Dytiscidae* (1), and *Hydrophilidae* (16); the beetles and the *Odonata* could have been caught out of water, either on low vegetation or on the ground.

In both seasons the differences among the amounts of various prey eaten were statistically significant. During the wet season *Coleoptera*, *Hemiptera*,

TABLE 44. — **Taxonomic composition of food occurring in 119 stomachs of *Phrynobatrachus perpalmatus* from the Parc National de l'Upemba.**

Number of stomachs in which nine principal groups occurred given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

- **Crustacea.** — *Isopoda.*
- **Arachnida.**
  - *Acarina.*
  - *Araneida.*
- **Chilopoda.**
  - *Scolopendridae.*
- **Diplopoda.**
- **Insecta.**
  - *Collembola.*
    - *Hypogastruridae.*
  - *Odonata.*
  - *Blattaria* (8).
  - *Orthoptera* (20).
    - *Gryllidae.*
    - *Tetrigidae.*
  - *Dermaptera.*
  - *Isoptera* (1).
    - *Termitidae.*
  - *Hemiptera* (48).
    - *Cercopidae.*
    - *Cicadellidae.*
    - *Fulgoridae.*
    - *Gerridae.*
    - *Jassidae.*
    - *Lygaeidae.*
    - *Miridae.*
    - *Pyrrhocoridae.*
    - *Veliidae.*
  - *Lepidoptera* (12).
    - *Arctiidae.*
    - *Phalaenidae.*
  - *Diptera* (29).
    - *Anthomyiidae.*
    - *Calliphoridae.*
    - *Chironomidae.*
    - *Culicidae.*
    - *Diopsidae.*
    - *Muscidae.*
    - *Mycetophilidae.*
    - *Sarcophagidae.*
    - *Sepsidae.*
    - *Syrphidae.*
    - *Tachinidae.*
    - *Tipulidae.*
    - *Trypetidae.*
  - *Coleoptera* (65).
    - *Anthicidae.*
    - *Carabidae.*
    - *Chrysomelidae.*
    - *Coccinellidae.*
    - *Curculionidae.*
    - *Dytiscidae.*
    - *Elateridae.*
    - *Erotylidae.*
    - *Hydrophilidae.*
    - *Limnichidae.*
    - *Melyridae.*
    - *Pselaphidae.*
    - *Ptiliidae.*
    - *Scarabaeidae.*
    - *Scolytidae.*
    - *Scydmaenidae.*
    - *Staphylinidae.*
    - *Tenebrionidae.*
  - *Hymenoptera.*
    - *Chalcidoidea.*
    - *Formicidae* (36).
    - *Scoliidae.*
    - *Sphecidae.*

and *Araneida* were eaten in the greatest amounts (deviation from uniformity significant at 0.001 level). During the dry season *Diptera*, *Hemiptera*, and *Coleoptera* dominated the diet (deviation from uniformity significant at 0.003 level).

Seasonal changes in the diet (Table 45) were extensive, involving at least two, and possibly four, of the five prey groups tested.

TABLE 45.

Seasonal variation in volume of given prey eaten by *Phrynobatrachus perpalmatus* in the Parc National de l'Upemba.

Probabilities for significant variations given in italics.

Prey	P	Season of greater consumption
Formicidae	*0.011*	Wet
Coleoptera	0.056	Wet
Hemiptera	0.45	Wet
Diptera	*0.01*	Dry
Araneida	0.052	Wet

In 50 stomachs chosen at random, the average volume of prey varied from 0.0005 to 0.160 ml (median 0.0154 ml). Total volume of prey in these stomachs ranged from 0.0005 (1 item) to 0.26 ml (3 items). Only four stomachs contained more than 9 items; one had 10, two had 11, and one had 22 items.

The frogs from which the 50 stomachs were taken had snout-vent lengths of 19.8 to 29.2 mm (median 23.0 mm). The size of the frog was not associated with the average volume of prey (Spearman rank correlation = −0.095).

Phrynobatrachus parvulus.

The 478 stomachs examined had the following distribution :

Meters	585-750	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	82	—	85	—	58	30
Dry season	—	84	63	20	36	20

The taxonomic composition of the diet is given in Table 46. The few aquatic types appeared in less thans 4 % of the stomachs : *Ephemeroptera* nymph (in one stomach), *Gerridae* (4), *Dytiscidae* (2), and *Hydrophilidae* (9).

The various prey categories were not eaten in equal amounts. Statistically significant deviation from uniformity was found in almost every season and elevation (Table 47). *Formicidae*, *Coleoptera*, *Hemiptera*, and *Diptera* dominated the diet in that order. *Isoptera* did not form a significant portion of the diet even during the wet season at the lowest elevations where they were abundant, if we can judge by the amounts eaten by *P. gutturosus* and *P. natalensis*.

TABLE 46. — **Taxonomic distribution of food occurring in 478 stomachs of *Phrynobatrachus parvulus* collected in the Parc National de l'Upemba.**

Number of stomachs containing nine principal groups given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.

Acarina.
Araneida (62).
Chelonethida. — *Ideoroncidae.*

Chilopoda. — *Geophilomorpha.*

Insecta.

Collembola.
Entomobryidae.
Ephemeroptera.
Palingeniidae.
Blattaria (7).
Orthoptera (23).
Gryllidae.
Tetrigidae.
Dermaptera.
Isoptera (13).
Termitidae.
Hemiptera (187).
Aphididae.
Cicadellidae.
Coreidae.
Fulgoridae.
Gerridae.
Hebridae.
Lygaeidae.
Miridae.
Pentatomidae.
Ploiariidae.
Psyllidae.
Reduviidae.
Saldidae.
Veliidae.
Trichoptera.
Lepidoptera (10).
Heterocera.
Phalaenidae.
Diptera (135).
Anthomyidae.
Bibionidae.
Calliphoridae.
Celyphidae.
Chironomidae.
Culicidae.
Diopsidae.
Dolichopodidae.
Drosophilidae.
Empididae.
Lonchopteridae.
Muscidae.
Mydaidae.
Phoridae.
Phryneidae.
Piophilidae.
Pipunculidae.
Sarcophagidae.
Scatopsidae.
Sciomyzidae.
Scopeumatidae.
Stratiomyidae.
Simuliidae.
Syrphidae.
Therevidae.
Tipulidae.
Trypetidae.
Coleoptera (173).
Anobiidae.
Anthicidae.
Buprestidae.
Carabidae.
Chrysomelidae.
Coccinellidae.
Cucujidae.
Curculionidae.
Cyphonidae.
Dermestidae.
Dytiscidae.
Elateridae.
Georyssidae.
Histeridae.
Hydrophilidae.
Languriidae.
Lathrididae.
Limnichidae.
Nitidulidae.
Orthoperidae.
Pselaphidae.
Scaphidiidae.
Scarabaeidae.
Scolytidae.
Scydmaenidae.

Staphylinidae.
Tenebrionidae.
Throscidae.
Hymenoptera.
Braconidae.
Ceraphronidae.
Chalcidae.
Diapriidae.
Eurytomidae.
Formicidae (225).
Ichneumonidae.
Mymaridae.
Platygasteridae.
Scelionidae.
Sphecidae.

TABLE 47. — **Test of uniformity of diet of** *Phrynobatrachus parvulus* **from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from uniformity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	*0.003*	*Formicidae, Hemiptera, Coleoptera*
751–1,000	Dry	< *0.001*	*Formicidae, Coleoptera, Hemiptera*
1,001–1,250	Wet	< *0.001*	*Formicidae, Hemiptera, Diptera*
1,001–1,250	Dry	< *0.001*	*Coleoptera, Hemiptera, Diptera*
1,251–1,500	Dry	0.09	*Formicidae, Diptera, Coleoptera*
1,501–1,750	Wet	< *0.001*	*Formicidae, Hemiptera, Coleoptera*
1,501–1,750	Dry	< *0.001*	*Coleoptera, Diptera, Formicidae*
1,751–1,830	Wet	0.07	*Hemiptera, Formicidae, Coleoptera*
1,751–1,830	Dry	0.14	*Coleoptera, Formicidae, Diptera*

Seasonal changes (Table 48) in the diet could be tested only in three altitudinal zones because of the distribution of stomachs examined (see above). *Coleoptera* show the greatest amount of seasonal variation, *Formicidae* and *Hemiptera* somewhat less, and *Diptera* none at all.

Altitudinal variation in amounts of a given prey eaten was evident in *Formicidae*, *Coleoptera*, and *Hemiptera* (Table 49). Larger amounts were eaten at the middle altitudes.

The average volume of food organisms in 50 stomachs chosen at random varied from 0.0001 to 0.020 ml (median 0.0027). The total volume of food in these stomachs varied between 0.0001 (1 item) and 0.087 ml (6 items). Ten stomachs contained one item, thirteen 2, fourteen 3 to 5, six 6 to 10, four 11 to 20, and one 53. The largest prey occurred in a stomach holding 2 items.

Snout-vent lengths of the 50 frogs from which these stomachs came had a range of 12.6-22.0 mm (median 17.1 mm). The Spearman rank correlation of snout-vent to average volume within stomachs of individual prey was +0.248, which is statistically significant (P = 0.03).

TABLE 48.

Seasonal variation in volume of given prey eaten by *Phrynobatrachus parvulus* **in the Parc National de l'Upemba.**

Probabilities for significant variations given in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	1,001–1,250	< *0.001*	Wet
Formicidae	1,501–1,750	0.10	Wet
Formicidae	1,751–1,830	0.82	Dry
Coleoptera	1,001–1,250	< *0.001*	Dry
Coleoptera	1,501–1,750	0.12	Dry
Coleoptera	1,751–1,830	< *0.001*	Dry
Hemiptera	1,001–1,250	*0.004*	Wet
Hemiptera	1,501–1,750	0.10	Wet
Hemiptera	1,751–1,830	0.33	Dry
Diptera	1,001–1,250	0.48	Wet
Diptera	1,501–1,750	0.62	Wet
Diptera	1,751–1,830	0.84	Dry

TABLE 49.

Altitudinal variation in volume of given prey eaten by *Phrynobatrachus parvulus* **in the Parc National de l'Upemba.**

Probabilities for significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	*0.03*	1,001–1,250
Formicidae	Dry	*0.046*	751–1,000
Coleoptera	Wet	0.80	1,501–1,750
Coleoptera	Dry	*0.04*	1,001–1,250
Hemiptera	Wet	*0.01*	1,001–1,250
Hemiptera	Dry	0.70	1,001–1,250
Diptera	Wet	0.28	1,501–1,750
Diptera	Dry	0.32	1,501–1,750

Phrynobatrachus gutturosus.

The stomachs examined had the following distribution :

Meters	585-750	751-1,000	1,001-1,250	1,251-1,500
Wet season	22	36	81	—
Dry season	—	16	10	4

The taxonomic composition of the diet is given in Table 50. Very few aquatic or partially aquatic groups are listed; among them are the *Hemiptera, Veliidae* and *Salidae*, which are riparian, and the *Hydrophilidae* and *Limnichidae* of the *Coleoptera.*

Significant deviation from uniformity was found only in the wet season of the three lowest altitudinal zones (Table 51). *Formicidae* were clearly the most important type of prey not only in terms of volume consumed (Table 51), but also in terms of the number of stomachs containing ants (Table 50). Next in order of importance were *Coleoptera, Isoptera,* and *Hemiptera.* As in the case of *P. natalensis, Isoptera* were important prey only during the wet seasons of the two lowest altitudinal zones; only 4 of the 33 termite-containing stomachs held imagos.

The distribution of stomachs examined limited analysis of seasonal variation to elevations between 751 and 1,250 m (Table 52). Statistically significant seasonal changes in diet were restricted to *Formicidae, Coleoptera,* and *Isoptera.* Significant altitudinal variation (Table 53) was found only in *Formicidae* and *Hemiptera.*

Average volume of food organisms in 50 stomachs chosen at random varied from 0.0009 to 0.130 ml (median 0.0038 ml). Total volume per stomach in these 50 ranged between 0.001 (1 item) and 0.130 ml (1 item). Nine stomachs contained only a single food organism, five held 2, nineteen 3 to 5, nine 6 to 10, six 11 to 20, one 22, and one 24. The smallest prey occurred in a stomach containing 8 items; the largest occurred alone.

Snout-vent lengths of these 50 frogs varied between 17.4 and 24.6 mm. Size of the predator bore no relationship to the average volume within stomachs of individual prey (Spearman correlation coefficient = -0.068).

TABLE 50. — **Taxonomic composition of food occurring in 169 stomachs of *Phrynobatrachus gutturosus* collected in the Parc National de l'Upemba.**

Number of stomachs in which nine principal groups occurred given in parentheses.

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea.

Isopoda.
- *Armadillidiidae.*
- *Porcellionidae.*

Arachnida.

Acarina.
Araneida (27).
Chelonethida.

Chilopoda.

- *Scolopendridae.*

Insecta.

Collembola.
- *Entomobryidae.*

Blattaria (2).
Orthoptera (7).
- *Gryllidae.*
- *Tetrigidae.*

Isoptera (33).
- *Termitidae.*

Thysanoptera.
- *Urothripidae.*

Hemiptera (41).
- *Aphididae.*
- *Areopodidae.*
- *Cicadellidae.*
- *Fulgoridae.*
- *Miridae.*
- *Nabidae.*
- *Pentatomidae.*
- *Reduviidae.*
- *Saldidae.*
- *Veliidae.*

Lepidoptera (2).
Diptera (21).
- *Anthomyidae.*
- *Bibionidae.*
- *Chironomidae.*
- *Drosophilidae.*
- *Lauxaniidae.*
- *Phoridae.*
- *Piophilidae.*
- *Sciomyzidae.*
- *Stratiomyidae.*
- *Syrphidae.*
- *Tachinidae.*
- *Tipulidae.*
- *Trixoscelidae.*

Coleoptera (46).
- *Anthicidae.*
- *Aphodiidae.*
- *Chrysomelidae.*
- *Curculionidae.*
- *Cyphonidae.*
- *Elateridae.*
- *Hydrophilidae.*
- *Limnichidae.*
- *Nitidulidae.*
- *Orthoperidae.*
- *Ptilliidae.*
- *Scarabaeidae.*
- *Scolytidae.*
- *Scydmaenidae.*
- *Staphylinidae.*
- *Tenebrionidae.*

Hymenoptera.
- *Apidae.*
- *Chrysididae.*
- *Eurytomidae.*
- *Evaniidae.*
- *Formicidae* (109).
- *Mymaridae.*
- *Platygasteridae.*
- *Sphecidae.*

TABLE 51. — **Test of uniformity of diet of *Phrynobatrachus gutturosus* from the Parc National de l'Upemba.**

Probabilities for statistically significant deviations from homogeneity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	< *0.001*	*Formicidae, Isoptera, Coleoptera*
751–1,000	Wet	< *0.001*	*Formicidae, Isoptera, Coleoptera*
751–1,000	Dry	0.08	*Formicidae, Coleoptera, Hemiptera*
1,001–1,250	Wet	< *0.001*	*Formicidae, Hemiptera, Coleoptera*
1,001–1,250	Dry	0.42	*Coleoptera, Araneida, Hemiptera*

TABLE 52.

Seasonal variation in the amounts of given prey eaten by *Phrynobatrachus gutturosus* in the Parc National de l'Upemba.

Probabilities for significant variations given in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	751–1,000	0.30	Wet
Formicidae	1,001–1,250	*0.004*	Wet
Coleoptera	751–1,000	0.69	Dry
Coleoptera	1,001–1,250	*0.02*	Dry
Hemiptera	751–1,000	0.15	Dry
Hemiptera	1,001–1,250	0.68	Wet
Diptera	751–1,000	0.64	Dry
Diptera	1,001–1,250	0.17	Wet
Araneida	751–1,000	0.71	Dry
Araneida	1,001–1,250	0.19	Dry
Isoptera	751–1,000	*0.03*	Wet

TABLE 53.

Altitudinal variation in volume of given prey eaten by *Phrynobatrachus gutturosus* **in the Parc National de l'Upemba.**

Probabilities for significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	0.17	585– 750
Formicidae	Dry	*0.03*	751–1,000
Coleoptera	Wet	0.10	751–1,000
Coleoptera	Dry	0.20	1,251–1,500
Hemiptera	Wet	< *0.001*	1,001–1,250
Hemiptera	Dry	0.52	1,251–1,500
Diptera	Wet	0.79	1,001–1,250
Araneida	Wet	0.70	751–1,000
Araneida	Dry	0.31	1,251–1,500
Isoptera	Wet	0.15	751–1,000

Phrynobatrachus natalensis.

Some stomachs containing food were available from all altitudes and seasons; the frequency distribution is given below :

Meters	585-750	751-1,000	1,001-1,250	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	136	44	85	28	36	18
Dry season	38	87	48	20	12	27

The taxonomic distribution of the food is given in Table 54. The great bulk of the organisms eaten was terrestrial. Of the 579 stomachs, only seven held aquatic *Coleoptera* (*Dryopidae*, *Dytiscidae*, and *Hydrophilidae*), eight held aquatic *Hemiptera* (*Belastomatidae*, *Hydrometridae*, and *Gerridae*), five *Odonata* nymphs, two *Ephemeroptera* nymphs, and two *Trichoptera* larvae.

Significant deviations from uniformity of diet were almost confined to the two lowest altitudinal zones (Table 55). *Formicidae*, *Isoptera*, and *Coleoptera* were the three most important types of prey with *Hemiptera* and *Diptera* forming a second level of somewhat less important prey.

TABLE 54. — **Taxonomic composition of food occurring in 579 stomachs of *Phrynobatrachus natalensis* collected in the Parc National de l'Upemba.**

Number of stomachs in which nine principal groups occurred given in parentheses.

ANNELIDA. — **Oligochaeta.**

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Crustacea. — *Isopoda.*

Arachnida.

Acarina.
Araneida (98).
Phalangida.

Chilopoda.

Geophilomorpha.
Scolopendridae.

Diplopoda.

Insecta.

Collembola.
Entomobryidae.
Ephemeroptera.
Palingeniidae.
Odonata.
Gomphidae.
Lestidae.
Metapodagrionidae.
Blattaria (59).
Orthoptera (59).
Acrididae.
Gryllidae.
Tetrigidae.
Tettigoniidae.
Dermaptera.
Isoptera (118).
Kalotermitidae.
Rhinotermitidae.
Termitidae.
Hemiptera (103).
Belastomatidae.
Cicadellidae.
Clastopteridae.
Corizidae.
Cydnidae.
Fulgoridae.
Gerridae.
Heniocephalidae.
Hydrometridae.
Lygaeidae.
Miridae.
Nabidae.
Ochteridae.
Pentatomidae.
Plataspidae.
Ploiariidae.
Pyrrhocoridae.
Reduviidae.
Thaumastotheriidae.
Tingidae.
Veliidae.
Trichoptera.
Rhyacophilidae.
Lepidoptera (51).
Arctiidae.
Geometridae.
Notodontidae.
Phalaenidae.
Diptera (82).
Asilidae.
Bibionidae.
Calliphoridae.
Ceratopogonidae.
Chironomidae.
Culicidae.
Diopsidae.
Dolicopodidae.
Drosophilidae.
Muscidae.
Mycetophilidae.
Phoridae.
Sarcophagidae.
Stratiomyidae.
Syrphidae.
Tabanidae.
Tipulidae.
Trypetidae.
Xylophagidae.
Coleoptera (145).
Anthicidae.
Bostrichidae.
Buprestidae.
Carabidae.
Chrysomelidae.
Coccinellidae.
Colydiidae.
Cryptophagidae.
Curculionidae.
Dermestidae.

Dytiscidae.
Elateridae.
Hydrophilidae.
Lampyridae.
Languriidae.
Limnichidae.
Melandryidae.
Mordellidae.
Nitidulidae.
Pselaphidae.
Ptinidae.
Scarabaeidae.
Scolytidae.
Scydmaenidae.
Staphylinidae.
Tenebrionidae.
Hymenoptera.
Apidae.
Braconidae.
Chalcidoidea.
Formicidae (288).
Mutillidae.
Sphecidae.
Tiphiidae.

AMPHIBIA (2).

TABLE 55. — **Test of uniformity of diet of** *Phrynobatrachus natalensis* **from Parc National de l'Upemba.**

Probabilities for statistically significant deviation from homogeity are in italics.

Altitude	Season	P	Principal food categories
585– 750	Wet	< *0.001*	*Formicidae, Isoptera, Coleoptera*
585– 750	Dry	< *0.001*	*Isoptera, Formicidae, Coleoptera*
751–1,000	Wet	< *0.001*	*Formicidae, Isoptera, Hemiptera*
751–1,000	Dry	< *0.001*	*Formicidae, Diptera, Coleoptera*
1,001–1,250	Wet	0.40	*Formicidae, Araneida, Miscellaneous*
1,001–1,250	Dry	*0.04*	*Coleoptera, Hemiptera, Formicidae*
1,251–1,500	Wet	0.20	*Formicidae, Araneida, Lepidoptera*
1,251–1,500	Dry	0.06	*Coleoptera, Hemiptera, Formicidae*
1,501–1,750	Wet	0.92	*Formicidae, Coleoptera, Hemiptera*
1,501–1,750	Dry	0.15	*Formicidae, Diptera, Araneida*
1,751–1,830	Wet	0.08	*Formicidae, Miscellaneous, Coleoptera*
1,751–1,830	Dry	0.23	*Formicidae, Coleoptera, Araneida*

Seasonal variation appeared in the amounts eaten of six kinds of prey (Table 56). *Formicidae* showed statistically significant deviation only in the lowest altitudinal zone in which more were eaten by *natalensis* during the wet season. As *Formicidae* are abundant in the savanna at all times, this difference is not easily explained. The larger amounts of *Isoptera* eaten during the rainy season is not related to their reproductive flights at 585-750 m, for only 8 of 54 termite-containing stomachs of that season

TABLE 56. — **Seasonal variation in the diet of *Phrynobatrachus natalensis* from the Parc National de l'Upemba.**

Probabilities for statistically significant variations given in italics.

Prey	Altitude	P	Season of greater consumption
Formicidae	585– 750	*0.008*	Wet
Formicidae	751–1,000	0.18	Wet
Formicidae	1,001–1,250	0.47	Wet
Formicidae	1,251–1,500	0.23	Wet
Formicidae	1,501–1,750	0.39	Wet
Formicidae	1,751–1,830	0.34	Wet
Isoptera	585– 750	*0.008*	Wet
Isoptera	751–1,000	< *0.001*	Wet
Isoptera	1,001–1,250	0.16	Dry
Isoptera	1,251–1,500	0.075	Wet
Isoptera	1,501–1,750	0.23	Wet
Isoptera	1,751–1,830	0.15	Wet
Coleoptera	585– 750	0.054	Wet
Coleoptera	751–1,000	0.19	Dry
Coleoptera	1,001–1,250	*0.009*	Dry
Coleoptera	1,251–1,500	*0.03*	Dry
Coleoptera	1,501–1,750	0.52	Dry
Coleoptera	1,751–1,830	0.30	Wet
Hemiptera	585– 750	0.50	Wet
Hemiptera	751–1,000	0.67	Dry
Hemiptera	1,001–1,250	0.054	Dry
Hemiptera	1,251–1,500	*0.028*	Dry
Hemiptera	1,501–1,750	0.65	Wet
Diptera	585– 750	*0.002*	Dry
Diptera	751–1,000	*0.028*	Dry
Diptera	1,001–1,250	0.88	Dry

TABLE 56 *(Continued.)*

Prey	Altitude	P	Season of greater consumption
Diptera	1,251-1,500	0.72	Dry
Diptera	1,501-1,750	0.27	Wet
Diptera	1,751-1,830	0.52	Wet
Araneida	1,001-1,250	*0.016*	Wet
Araneida	1,251-1,500	0.46	Wet
Araneida	1,501-1,750	0.20	Wet
Araneida	1,751-1,830	0.70	Dry

TABLE 57.

Altitudinal variation in volume of given prey eaten by *Phrynobatrachus natalensis* in the Parc National de l'Upemba.

Probabilities for significant variations given in italics.

Prey	Season	P	Altitude of maximum consumption
Formicidae	Wet	*0.01*	751-1,000
Formicidae	Dry	0.22	751-1,000
Isoptera	Wet	< *0.001*	585- 750
Isoptera	Dry	0.10	585- 750
Coleoptera	Wet	0.10	1,751-1,830
Coleoptera	Dry	*0.044*	1,251-1,500
Hemiptera	Wet	0.40	1,501-1,750
Hemiptera	Dry	< *0.001*	1,251-1,500
Diptera	Wet	0.065	1,001-1,250
Diptera	Dry	0.75	1,501-1,750

and altitude held imagos. On the other hand, 12 of 20 stomachs from the wet season at 751-1,000 m contained imagos. Not enough termites were eaten by *natalensis* above 1,000 m to show seasonal variation.

Altitudinal variation in the consumption of given food categories is statistically significant during the wet season for *Isoptera* and *Formicidae* and during the dry season for *Coleoptera* and *Hemiptera* (Table 57).

TABLE 58.

Significant deviations from uniformity in diets of species of *Phrynobatrachus* from the Parc National de l'Upemba.

Species	Altitude	Season	Dominant food
natalensis	585– 750	Wet	*Formicidae, Isoptera, Coleoptera*
gutturosus	585– 750	Wet	*Formicidae, Isoptera, Coleoptera*
parvulus	585– 750	Wet	*Formicidae, Hemiptera, Coleoptera*
cryptotis	585– 750	Wet	*Formicidae, Araneida, Coleoptera*
perpalmatus	585– 750	Wet	*Coleoptera, Hemiptera, Araneida*
natalensis	585– 750	Dry	*Isoptera, Formicidae, Coleoptera*
perpalmatus	585– 750	Dry	*Diptera, Hemiptera, Coleoptera*
natalensis	751–1,000	Wet	*Formicidae, Isoptera, Hemiptera*
gutturosus	751–1,000	Wet	*Formicidae, Isoptera, Coleoptera*
natalensis	751–1,000	Dry	*Formicidae, Diptera, Coleoptera*
parvulus	751–1,000	Dry	*Formicidae, Coleoptera, Hemiptera*
parvulus	1,001–1,250	Wet	*Formicidae, Hemiptera, Diptera*
gutturosus	1,001–1,250	Wet	*Formicidae, Hemiptera, Coleoptera*
natalensis	1,001–1,250	Dry	*Coleoptera, Hemiptera, Formicidae*
parvulus	1,001–1,250	Dry	*Coleoptera, Hemiptera, Diptera*
parvulus	1,501–1,750	Wet	*Formicidae, Hemiptera, Coleoptera*
cryptotis	1,501–1,750	Wet	*Hemiptera, Coleoptera, Formicidae*
parvulus	1,501–1,750	Dry	*Coleoptera, Diptera, Formicidae*
anotis	1,501–1,750	Dry	*Formicidae, Coleoptera, Diptera*
cryptotis	1,751–1,830	Wet	*Coleoptera, Formicidae, Hemiptera*
anotis	1,751–1,830	Wet	*Coleoptera, Araneida, Formicidae*
cryptotis	1,751–1,830	Dry	*Hemiptera, Coleoptera, Diptera*

TABLE 59.

Significant seasonal variation in quantities of given prey eaten by species of *Phrynobatrachus* in the Parc National de l'Upemba.

Species	Altitude	Food	Season of greater consumption
natalensis	585– 750	*Formicidae*	Wet
natalensis	585– 750	*Isoptera*	Wet
natalensis	585– 750	*Diptera*	Dry
perpalmatus	585– 750	*Diptera*	Dry
perpalmatus	585– 750	*Formicidae*	Wet
perpalmatus	585– 750	*Araneida*	Wet
perpalmatus	585– 750	*Coleoptera*	Wet
natalensis	751–1,000	*Isoptera*	Wet
natalensis	751–1,000	*Diptera*	Dry
natalensis	1,001–1,250	*Coleoptera*	Dry
natalensis	1,001–1,250	*Araneida*	Wet
parvulus	1,001–1,250	*Coleoptera*	Dry
parvulus	1,001–1,250	*Hemiptera*	Wet
parvulus	1,001–1,250	*Formicidae*	Wet
gutturosus	1,001–1,250	*Formicidae*	Wet
gutturosus	1,001–1,250	*Coleoptera*	Dry
natalensis	1,251–1,500	*Coleoptera*	Dry
natalensis	1,251–1,500	*Hemiptera*	Dry
cryptotis	1,501–1,750	*Formicidae*	Wet
cryptotis	1,751–1,830	*Formicidae*	Wet
cryptotis	1,751–1,830	*Coleoptera*	Wet
parvulus	1,751–1,830	*Coleoptera*	Dry
anotis	1,751–1,830	*Coleoptera*	Dry
anotis	1,751–1,830	*Formicidae*	Wet

TABLE 60.

Significant altitudinal variation in the volumes of given prey eaten by species of *Phrynobatrachus* in the Parc National de l'Upemba.

Species	Season	Food	Altitude of maximum consumption
natalensis	Wet	*Isoptera*	585– 750
natalensis	Wet	*Formicidae*	751–1,000
gutturosus	Wet	*Hemiptera*	1,001–1,250
cryptotis	Wet	*Formicidae*	585– 750
cryptotis	Wet	*Coleoptera*	1,751–1,830
cryptotis	Wet	*Diptera*	1,001–1,250
cryptotis	Wet	*Hemiptera*	1,501–1,750
parvulus	Wet	*Formicidae*	1,001–1,250
parvulus	Wet	*Hemiptera*	1,001–1,250
natalensis	Dry	*Coleoptera*	1,251–1,500
natalensis	Dry	*Hemiptera*	1,251–1,500
gutturosus	Dry	*Formicidae*	751–1,000
anotis	Dry	*Formicidae*	1,501–1,750
cryptotis	Dry	*Hemiptera*	1,751–1,830
parvulus	Dry	*Formicidae*	751–1,000
parvulus	Dry	*Coleoptera*	1,001–1,250

Conceivably the greater amounts of the last two types of prey eaten above 1,000 m may reflect the decreasing availability of *Isoptera*. When *Isoptera* are abundant, *natalensis* may feed on them and *Formicidae* and turn increasingly to other foods as one of the two becomes less abundant.

Average volume of food organisms in 50 stomachs chosen at random varied from 0.001 to 0.200 ml (median 0.0205 ml). Total volume per stomachs ranged between 0.001 (1 item) and 0.502 ml (4 items). Twelve stomachs contained one prey organism, four 2, twenty-one 3 to 5, five 6 to 10, one 11, four 21 to 30, two 31 to 50, and one 154. The smallest prey occurred in a stomach containing 25 organisms and the largest occurred alone.

Snout-vent length of the 50 frogs varied from 26.1 to 37.5 mm. Correlation between predator snout-vent and average volume within stomachs of individual prey is +0.286, which is statistically significant ($P = 0.01$).

SUMMARY OF PHRYNOBATRACHUS SPECIES.

Some striking similarities among the diets of species in this genus appear in Table 58. The overwhelming importance of *Formicidae* and the slightly lesser importance of *Coleoptera*, *Hemiptera*, and *Diptera*, in that order, characterize almost all of the diets. The outstanding exception to that order of food dominance is the relative insignificance of *Formicidae* in the diet of *perpalmatus*. The most likely explanation for this exception is the near absence of *Formicidae* from the aquatic habitat of *perpalmatus*.

In general availability is sufficient explanation for the dominance of the categories in Table 58, for they include the most abundant groups of terrestrial invertebrates. *Acarina* and *Collembola* may be more abundant than *Formicidae* and the others, but their extremely small size may eliminate them to all practical purposes from the diets of predators as large as adult amphibians. They appear in only a few stomachs of *Phrynobatrachus*.

Availability is probably the explanation also for the restriction of *Isoptera* as important prey to elevations below 1,000 m; the abundance of *Isoptera* drops off rapidly at high altitudes.

Each species of *Phrynobatrachus* showed some seasonal variation in diet (Table 59). *Formicidae* were eaten in greater volumes in the wet season; this family appears 7 times in Table 59 and invariably the rainy season is the season of greater consumption. *Coleoptera* were eaten in larger amounts during the dry season in six of their eight appearances in Table 59. *Diptera* were likewise eaten in larger amounts in the dry season in all instances of significant seasonal change. Though they appear in Table 59 only twice, *Isoptera* in both cases were more important in the wet season than in the dry, but not because of reproductive flights (see pp. 54 and 60).

The altitudinal variation summarized in Table 60 has one general pattern : *Formicidae* were eaten in larger amounts below 1,000 m and the other principal food categories above 1,000 m. Only three exceptions to this rule appear in Table 60. (1) The altitude of greatest consumption of *Formicidae* by *parvulus* was 1,001-1,250 m in the wet season. (2) *Phrynobatrachus anotis* ate more *Formicidae* at 1,501-1,750 m, but food-containing stomachs of this species were available only between 1,501 and 1,830 m. (3) *Isoptera* were eaten in greatest amounts by *natalensis* at the lowest elevation, a consequence of the limited altitudinal distribution of *Isoptera*.

The complementary relationship between *Formicidae* on the one hand and the other principal food categories on the other in both seasonal and altitudinal variation suggests again the role of availability in determining the diet. When *Formicidae* were active, they were eaten in large amounts and consumption of other prey was correspondingly reduced.

Direct comparison of the diets of *Phrynobatrachus* species must be undertaken one food category, at one altitude, and during one season at a time (Table 61). Except in the 585-750 m zone during the wet season,

TABLE 61. — **Significant differences among species of** *Phrynobatrachus* **in the Parc National de l'Upemba in volumes of given prey eaten.**

Food	Altitude	Season	P	Species compared, in order of decreasing consumption
Formicidae	585– 750	Wet	<0.001	*gutturosus, cryptotis, natalensis, parvulus, perpalmatus*
Coleoptera	585– 750	Wet	<0.001	*perpalmatus, parvulus, natalensis, gutturosus, cryptotis*
Hemiptera	585– 750	Wet	0.009	*perpalmatus, parvulus, natalensis, gutturosus, cryptotis*
Diptera	585– 750	Wet	0.009	*parvulus, perpalmatus, gutturosus, natalensis, cryptotis*
Isoptera	585– 750	Wet	<0.001	*natalensis, gutturosus, cryptotis, parvulus, perpalmatus*
Formicidae	585– 750	Dry	0.024	*natalensis, perpalmatus*
Hemiptera	585– 750	Dry	0.003	*parpalmatus, natalensis*
Diptera	585– 750	Dry	0.036	*perpalmatus, natalensis*
Coleoptera	751–1,000	Wet	0.044	*gutturosus, natalensis*
Hemiptera	751–1,000	Dry	0.03	*parvulus, gutturosus, natalensis, cryptotis*
Hemiptera	1,001–1,250	Wet	<0.001	*parvulus, gutturosus, natalensis*
Isoptera	1,001–1,250	Wet	<0.001	*gutturosus, natalensis, parvulus, cryptotis*
Coleoptera	1,251–1,500	Dry	0.04	*natalensis, cryptotis, parvulus*
Formicidae	1,751–1,830	Wet	0.008	*natalensis, anotis, parvulus*
Coleoptera	1,751–1,830	Wet	0.05	*anotis, natalensis, parvulus*
Hemiptera	1,751–1,830	Wet	0.027	*parvulus, anotis, natalensis*
Formicidae	1,751–1,830	Dry	0.017	*natalensis, parvulus, anotis*
Hemiptera	1,751–1,830	Dry	0.035	*anotis, parvulus, natalensis*

natalensis ate more *Formicidae* than any other species of *Phrynobatrachus*; this generalization applies to all altitudes and seasons in which the diets differ significantly. *Phrynobatrachus parvulus* consistently ate more *Hemiptera* than *gutturosus* and *natalensis*, about the same amount as *anotis*, and less than *permalmatus*. No species consistently ate more *Coleoptera* than the others. Only *gutturosus* and *natalensis* ate *Isoptera* in significant quantities.

These six species of *Phrynobatrachus* differ in the size of their prey (Table 71). The Kruskal-Wallis test applied to the six sets of 50 randomly-selected stomachs (referred to in the separate species' accounts) shows that the null hypothesis (no difference in prey size) may be safely rejected (= 61.15; $P < 0.001$). Only *natalensis* and *parvulus* show correlation between the length of the frog and the average volume of prey within stomachs. Though not large, +0.286 and +0.248, respectively, the correlations are significant ($P = 0.01$ and 0.03). The between-species correlation is much higher, the Spearman rank correlation coefficient of the snout-vent and average prey volume medians (see Table 71) being +0.94 ($P = 0.01$).

Inter-species correlation between predator and prey sizes helps to explain the fact that *natalensis* ate larger amounts of *Isoptera* than *anotis*, *parvulus*, and *cryptotis* as termites are among the largest prey. But since *gutturosus* is smaller than *perpalmatus*, the difference between *natalensis* and *gutturosus* on the one hand and *perpalmatus* on the other in the amount of termites eaten cannot be explained by differences in the sizes of the predators. The absence of termites from the aquatic habitat of *perpalmatus* is the most likly explanation.

Family RHACOPHORIDAE.

Genus KASSINA Girard.

Kassina senegalensis.

Food containing stomachs were removed from frogs having the following distribution :

Meters	585-750	1,251-1,500	1,501-1,750	1,751-1,830
Wet season	3	—	27	1
Dry season	—	21	—	1

The taxonomic distribution of the prey is given in Table 62. The diet consisted of terrestrial arthropods, many of them not very active (e.g., *Termitidae* and larvae of *Lepidoptera*). Although *Araneida*, *Hemiptera*, *Orthoptera*, and *Lepidoptera* were eaten in greater volumes at 1,251-1,500 m, the deviation of the diet from uniformity at that elevation is not statistically significant ($P = 0.10$). The deviation from uniformity is significant ($P < 1.001$) at 1,501-1,750 m, in which zone *Lepidoptera*, *Hemiptera*, and *Coleoptera* dominated the diet.

Seasonal and altitudinal variations could not be tested.

The average volume of individual prey within each of 50 stomachs varied from 0.004 to 0.100 ml (median = 0.030). The total volume of prey in these stomachs varied from 0.010 (1 item) to 0.393 ml (6 items). Seven stomachs contained one prey organism, fifteen 2, eleven 3 to 5, seven 6 to 10, six 11 to 20, three 23 to 30, and one 32.

Snout-vent lengths of these 50 frogs ranged from 21.8 to 38.7 mm (median 31.1). Correlation of snout-vent with average volume within stomachs of individual prey was high, the Spearman rank coefficient being +0.44 (P = 0.003).

TABLE 62.

Taxonomic distribution of prey in 58 stomachs of *Kassina senegalensis* from the Parc National de l'Upemba.

Numbers of stomachs containing particular prey given in parentheses.

ARTHROPODA.

Arachnida.

Acarina.
Araneida (24).

Insecta.

Blattaria (7).
Orthoptera (14).
Acrididae.
Gryllidae.
Manteidae.
Phasmatidae.
Tetrigidae.
Isoptera. — *Termitidae* (7).
Hemiptera (19).
Homoptera.
Cercopidae.
Cicadellidae.
Fulgoridae.
Hydrometridae.
Lygaeidae.
Pentatomidae.
Reduviidae.
Lepidoptera (21).
Diptera (17).
Calliphoridae.
Diopsidae.
Mycetophilidae.
Syrphidae.
Coleoptera (16).
Chrysomelidae.
Cleridae.
Curculionidae.
Elateridae.
Scarabaeidae.
Staphylinidae.
Hymenoptera.
Braconidae.
Formicidae (8).
Ichneumonidae.

Genus LEPTOPELIS GÜNTHER.

Leptopelis bocagei.

Only 14 food-containing stomachs were available. All were from frogs caught at 585-750 m, 12 during the wet season and 2 during the dry season. The taxonomic distribution of the prey is given in Table 63. Although the diet did not deviate significantly from uniformity (chi-square = 6.08; degrees of freedom = 9; P = 0.73), it is evident that *Orthoptera* were eaten in largest quantities. All *Termitidae* eaten were imagos. The presence of earthworms and chilopods in the diet suggests that a least part of the food was obtained on the ground.

The average volume of individual prey within the 14 stomachs varied from 0.04 to 0.35 ml (median 0.15). Total volume within stomachs ranged between 0.04 (1 item) and 8.27 ml (35 items). Seven stomachs each contained 1 item, three contained 2, one 4, one 6, one 7, and one 35.

Snout-vent length of the 14 frogs varied from 40.9 to 63.2 mm (median 51.1). Correlation of snout-vent with average volume within stomachs of individual prey is insignificant (Spearman rank coefficient = +0.075; P = 0.79).

TABLE 63.

Taxonomic distribution of prey found in 14 stomachs of *Leptopelis bocagei* **from the Parc National de l'Upemba.**

Number of stomachs containing specified food given in parentheses.

ANNELIDA. — **Oligochaeta** (2).

MOLLUSCA. — **Gastropoda.**

ARTHROPODA.

Chilopoda (3).
- *Geophilomorpha.*
- *Scolopendridae.*

Insecta.
- *Blattaria* (3).
- *Orthoptera* (8).
  - *Acrididae.*
  - *Gryllidae.*
  - *Tettigoniidae.*
- *Isoptera.* — *Termitidae* (2).
- *Lepidoptera* (2).
- *Coleoptera* (2).
  - *Cistelidae.*
  - *Scarabaeidae.*
- *Hymenoptera.*
  - *Formicidae* (1).

AMPHIBIA (1).

CONCLUSIONS.

One of the ways in which the three major genera (*Bufo*, *Rana*, *Phrynobatrachus*) differ is in the degree to which their diets are concentrated on one or several types of prey. Concentration rather than specialization is at issue here. If a frog feeds primarily on *Formicidae* at one season and altitude and on *Araneida* at another, one cannot say that it is a specialized feeder. But one can say that its diet is concentrated on one or a few foods as compared to a species that eats approximately equal amounts of six different prey types.

In Table 64 each season and altitude at which the diet of a species deviated significantly from uniformity (that is, showed concentration on one or a few foods) is indicated by the letter H; the letter U indicates no deviation from uniformity, or lack of concentration. As tests of uniformity (see p. 9) were run using only 8 to 12 prey categories omitting those orders not appearing in significant numbers, uniformity here is measured only in terms of those 8 to 12 categories.

Using the ratio of H's to U's within a genus as a measure of food concentration, *Bufo* (20 : 4) shows the most concentration, *Phrynobatrachus* (22 : 18) the next most, and *Rana* (6 : 19) the least. Only one species was studied in each of the other four genera, which, in terms of the ratio H : U, fall in the following order : *Arthroleptis* (3 : 1), *Xenopus* (4 : 3), *Kassina* (1 : 1), and *Leptopelis* (0 : 1).

Species and genera differ not only in the extent to which their diets are concentrated but also in the prey on which their diets are concentrated. Tables 65-69 show the seasons and altitudes at which given prey form a dominant element of the diet; only the most commonly eaten foods are considered. « Dominance » here is applied to the three taxonomic categories of prey eaten in greatest volumes in those instances of statistically significant deviation from uniformity as determined by the Friedman analysis of variance (p. 9). Consequently, in this discussion a particular prey can be a dominant only in those cells of Table 64 containing an H.

Tables 65-69 show that : *Formicidae* constitute a dominant primarily in frogs of the genera *Bufo*, *Arthroleptis*, and *Phrynobatrachus*; *Coleoptera* constitute a dominant in all genera, though less so in *Arthroleptis*; *Hemiptera* primarily in *Phrynobatrachus* and to a lesser extent in *Bufo* and *Rana*; *Isoptera* primarily in *Arthroleptis* and to a lesser extent in *Bufo* and *Phrynobatrachus;* and *Araneida* primarily in *Rana*. *Orthoptera* constitute a dominant food in one season-altitude each of *Xenopus laevis*, *Bufo regularis*, *Rana fuscigula*, *R. frontalis*, *R. grandisonae*, and *Arthroleptis stenodactylus*.

TABLE 64. — **Occurrence of heterogeneity in the diets of amphibians from the Parc National de l'Upemba.**

H = diet heterogeneous; U = diet uniform; — = no data.

	585-750 m		751-1,000 m		1,001-1,250 m		1,251-1,500 m		1,501-1,750 m		1,751-1,830 m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Xenopus laevis	H	U	—	U	H	—	—	—	H	—	H	U
Bufo regularis	H	H	H	U	H	H	U	H	H	—	U	H
Bufo funereus	—	—	H	H	U	H	H	H	H	H	H	H
Bufo ushoranus	—	—	H	—	—	—	H	—	—	—	—	—
Bufo melanopleura	—	—	—	—	—	—	H	—	—	—	—	—
Rana fuscigula	—	—	U	U	H	U	U	U	H	H	U	U
Rana frontalis	H	U	—	—	—	—	—	—	—	—	—	—
Rana mascareniensis	H	U	—	—	—	—	—	—	—	—	—	—
Rana grandisonae	—	—	—	—	—	—	—	U	U	—	H	U
Rana uzungwensis	—	—	—	—	—	—	—	U	—	—	U	—
Rana porosissima	—	—	—	—	—	—	—	U	U	U	U	U
Arthroleptis stenodactylus	H	—	H	—	H	—	U	—	—	—	—	—
Phrynobatrachus anotis	—	—	—	—	—	—	—	—	U	H	H	U
Phrynobatrachus cryptotis	H	—	—	U	U	—	—	U	H	U	H	H
Phrynobatrachus perpalmatus	H	H	—	—	—	—	—	—	—	—	—	—
Phrynobatrachus parvulus	H	—	—	H	H	H	—	U	H	H	U	U
Phrynobatrachus gutturosus	H	—	H	U	H	U	—	—	—	—	—	—
Phrynobatrachus natalensis	H	H	H	H	U	H	U	U	U	U	U	U
Kassina senegalensis	—	—	—	—	—	—	—	U	H	—	—	—
Leptopelis bocagei	U	—	—	—	—	—	—	—	—	—	—	—

TABLE 65. — **Importance of *Formicidae* in diets of amphibians in the Parc National de l'Upemba.**

+ = dominant (*); O = non-dominant; U = diet uniform; — = no data.

	585-750 m		751-1,000 m		1,001-1,250 m		1,251-1,500 m		1,501-1,750 m		1,751-1,830 m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Xenopus laevis	O	U	—	O	+	—	—	—	O	—	O	U
Bufo regularis	+	+	+	U	+	+	U	+	+	—	U	+
Bufo funereus	—	—	+	+	U	+	+	+	+	+	+	+
Bufo ushoranus	—	—	+	—	—	—	+	—	—	—	—	—
Bufo melanopleura	—	—	—	—	—	—	+	—	—	—	—	—
Rana fuscigula	—	—	U	U	+	U	U	U	O	O	U	U
Rana frontalis	O	U	—	—	—	—	—	—	—	—	—	—
Rana mascareniensis	O	U	—	—	—	—	—	—	—	—	—	—
Rana grandisonae	—	—	—	—	—	—	—	U	U	—	O	U
Rana uzungwensis	—	—	—	—	—	—	—	U	—	—	U	—
Rana porosissima	—	—	—	—	—	—	—	U	U	U	U	U
Arthroleptis stenodactylus	+	—	+	—	+	—	U	—	—	—	—	—
Phrynobatrachus anotis	—	—	—	—	—	—	—	—	U	+	+	U
Phrynobatrachus cryptotis	+	—	—	U	U	—	—	U	+	U	+	O
Phrynobatrachus perpalmatus	O	O	—	—	—	—	—	—	—	—	—	—
Phrynobatrachus parvulus	+	—	—	+	+	O	—	U	+	+	U	U
Phrynobatrachus gutturosus	+	—	+	U	+	U	—	—	—	—	—	—
Phrynobatrachus natalensis	+	+	+	+	U	+	U	U	U	U	U	U
Kassina senegalensis	—	—	—	—	—	—	—	U	O	—	—	—
Leptopelis bocagei	U	—	—	—	—	—	—	—	—	—	—	—

(*) « Dominance » explained in text.

TABLE 66. — **Importance of *Coleoptera* in diets of amphibians in the Parc National de l'Upemba.**

+ = dominant; O = non-dominant; U = diet uniform; — = no data.

	585-750 m		751-1,000 m		1,001-1,250 m		1,251-1,500 m		1,501-1,750 m		1,751-1,830 m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Xenopus laevis	+	U	—	O	+	—	—	—	+	—	+	U
Bufo regularis	+	+	+	U	+	+	U	+	+	—	U	+
Bufo funereus	—	—	+	+	U	+	+	+	+	+	+	+
Bufo ushoranus	—	—	+	—	—	—	+	—	—	—	—	—
Bufo melanopleura	—	—	—	—	—	—	+	—	—	—	—	—
Rana fuscigula	—	—	U	U	+	U	U	U	+	+	U	U
Rana frontalis	O	U	—	—	—	—	—	—	—	—	—	—
Rana mascareniensis	+	U	—	—	—	—	—	—	—	—	—	—
Rana grandisonae	—	—	—	—	—	—	—	U	U	—	+	U
Rana uzungwensis	—	—	—	—	—	—	—	U	—	—	U	—
Rana porosissima	—	—	—	—	—	—	—	U	U	U	U	U
Arthroleptis stenodactylus	O	—	O	—	+	—	U	—	—	—	—	—
Phrynobatrachus anotis	—	—	—	—	—	—	—	—	U	+	+	U
Phrynobatrachus cryptotis	+	—	—	U	U	—	—	U	+	U	+	+
Phrynobatrachus perpalmatus	+	+	—	—	—	—	—	—	—	—	—	—
Phrynobatrachus parvulus	+	—	—	+	O	+	—	U	+	+	U	U
Phrynobatrachus gutturosus	+	—	+	U	+	U	—	—	—	—	—	—
Phrynobatrachus natalensis	+	+	O	+	U	+	U	U	U	U	U	U
Kassina senegalensis	—	—	—	—	—	—	—	U	+	—	—	—
Leptopelis bocagei	U	—	—	—	—	—	—	—	—	—	—	—

TABLE 67. — **Importance of *Hemiptera* in diets of amphibians in the Parc National de l'Upemba.**

\+ = dominant; O = non-dominant; U = diet uniform; — = no data.

	585-750 m		751-1,000 m		1,001-1,250 m		1,251-1,500 m		1,501-1,750 m		1,751-1,830 m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Xenopus laevis	O	U	—	U	O	—	—	—	O	—	O	U
Bufo regularis	O	O	O	U	O	O	U	O	O	—	U	O
Bufo funereus	—	—	O	+	U	+	O	+	+	O	O	+
Bufo ushoranus	—	—	O	—	—	—	O	—	—	—	—	—
Bufo melanopleura	—	—	—	—	—	—	O	—	—	—	—	—
Rana fuscigula	—	—	U	U	O	U	U	U	O	+	U	U
Rana frontalis	O	U	—	—	—	—	—	—	—	—	—	—
Rana mascareniensis	+	U	—	—	—	—	—	—	—	—	—	—
Rana grandisonae	—	—	—	—	—	—	—	U	U	—	O	U
Rana uzungwensis	—	—	—	—	—	—	—	U	—	—	U	—
Rana porosissima	—	—	—	—	—	—	—	U	U	U	U	U
Arthroleptis stenodactylus	O	—	O	—	O	—	U	—	—	—	—	—
Phrynobatrachus anotis	—	—	—	—	—	—	—	—	U	O	O	U
Phrynobatrachus cryptotis	O	—	—	U	U	—	—	U	+	U	+	+
Phrynobatrachus perpalmatus	+	+	—	—	—	—	—	—	—	—	—	—
Phrynobatrachus parvulus	+	—	—	+	+	+	—	U	+	O	U	U
Phrynobatrachus gutturosus	O	—	O	U	+	U	—	—	—	—	—	—
Phrynobatrachus natalensis	O	O	+	O	U	+	U	U	U	U	U	U
Kassina senegalensis	—	—	—	—	—	—	—	U	+	—	—	—
Leptopelis bocagei	U	—	—	—	—	—	—	—	—	—	—	—

TABLE 68. — **Importance of *Isoptera* in diets of amphibians in the Parc National de l'Upemba.**

+ = dominant; O = non-dominant; U = diet uniform; — = no data.

	585-750 m		751-1,000 m		1,001-1,250 m		1,251-1,500 m		1,501-1,750 m		1,751-1,830 m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Xenopus laevis	O	U	—	U	O	—	—	—	O	—	+	U
Bufo regularis	+	O	+	U	+	O	U	O	O	—	U	O
Bufo funereus	—	—	O	O	U	O	O	O	O	O	O	O
Bufo ushoranus	—	—	+	—	—	—	+	—	—	—	—	—
Bufo melanopleura	—	—	—	—	—	—	+	—	—	—	—	—
Rana fuscigula	—	—	U	U	O	U	U	U	O	O	U	U
Rana frontalis	O	U	—	—	—	—	—	—	—	—	—	—
Rana mascareniensis	O	U	—	—	—	—	—	—	—	—	—	—
Rana grandisonae	—	—	—	—	—	—	—	U	U	—	O	U
Rana uzungwensis	—	—	—	—	—	—	—	U	—	—	U	—
Rana porosissima	—	—	—	—	—	—	—	U	U	U	U	U
Arthroleptis stenodactylus	+	—	+	—	+	—	U	—	—	—	—	—
Phrynobatrachus anotis	—	—	—	—	—	—	—	—	U	O	O	U
Phrynobatrachus cryptotis	O	—	—	U	U	—	—	U	O	U	O	O
Phrynobatrachus perpalmatus	O	O	—	—	—	—	—	—	—	—	—	—
Phrynobatrachus parvulus	O	—	—	O	O	O	—	U	O	O	U	U
Phrynobatrachus gutturosus	+	—	+	U	O	U	—	—	—	—	—	—
Phrynobatrachus natalensis	+	+	+	O	U	O	U	U	U	U	U	U
Kassina senegalensis	—	—	—	—	—	—	—	U	O	—	—	—
Leptopelis bocagei	U	—	—	—	—	—	—	—	—	—	—	—

TABLE 69. — **Importance of *Araneida* in diets of amphibians in the Parc National de l'Upemba.**

+ = dominant; O = non-dominant; U = diet uniform; — = no data.

	585-750 m		751-1,000 m		1,001-1,250 m		1,251-1,500 m		1,501-1,750 m		1,751-1,830 m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Xenopus laevis	O	U	—	U	O	—	—	—	O	—	O	U
Bufo regularis	O	+	O	U	O	O	U	O	O	—	U	+
Bufo funereus	—	—	+	O	U	O	O	O	O	O	O	O
Bufo ushoranus	—	—	O	—	—	—	O	—	—	—	—	—
Bufo melanopleura	—	—	—	—	—	—	O	—	—	—	—	—
Rana fuscigula	—	—	U	U	O	U	U	U	+	+	U	U
Rana frontalis	+	U	—	—	—	—	—	—	—	—	—	—
Rana mascareniensis	+	U	—	—	—	—	—	—	—	—	—	—
Rana grandisonae	—	—	—	—	—	—	—	U	U	—	+	U
Rana uzungwensis	—	—	—	—	—	—	—	U	—	—	U	—
Rana porosissima	—	—	—	—	—	—	—	U	U	U	U	U
Arthroleptis stenodactylus	O	—	O	—	O	—	U	—	—	—	—	—
Phrynobatrachus anotis	—	—	—	—	—	—	—	—	U	O	+	U
Phrynobatrachus cryptotis	+	—	—	U	U	—	—	U	O	U	O	O
Phrynobatrachus perpalmatus	+	O	—	—	—	—	—	—	—	—	—	—
Phrynobatrachus parvulus	O	—	—	O	O	O	—	U	O	O	U	U
Phrynobatrachus gutturosus	O	—	O	U	O	U	—	—	—	—	—	—
Phrynobatrachus natalensis	O	O	O	O	U	O	U	U	U	U	U	U
Kassina senegalensis	—	—	—	—	—	—	—	U	O	—	—	—
Leptopelis bocagei	U	—	—	—	—	—	—	—	—	—	—	—

Diptera are a dominant in two season-altitudes of *Xenopus laevis*, in one each of *Phrynobatrachus anotis*, *P. cryptotis*, and *P. perpalmatus*, and in three of *P. parvulus*.

The frequencies of dominant and non-dominant positions of these prey types are summarized in Table 70. Seasons and altitudes in which diets do not deviate significantly from uniformity are not included. Treating the frequencies of each prey type as separate contingency tables, statistically significant values of chi-square are obtained in every case.

The statement that two species or genera feed heavily on *Coleoptera* may obscure a difference in the diets. For example, *Xenopus laevis*, *Bufo regularis*, and *Rana fuscigula* eat large volumes of beetles, but *Xenopus* eats more aquatic forms than do the other two species. *Dytiscidae* were found in 15 stomachs of *Xenopus* and the much more abundant, terrestrial *Carabidae* only in 2. The numbers of stomachs of *B. regularis* in which these ecologically divergent beetles were found are, respectively, 2 and 59, and in *R. fuscigula* 1 and 39. Differences in the habits of the predators are the obvious explanation for these dietary differences : *B. regularis* customarily enters water only to breed; *R. fuscigula*, generally associated with the edges of streams and ponds (LOVERIDGE, 1936 : 410), evidently feeds along the banks as do most species of *Rana*; *Xenopus*, although it may emerge from water, usually feeds in water as do its relatives *Pipa* (RABB and SNEDIGAR, 1960) and *Hymenochirus*.

Intrageneric differences of the same sort appear in *Phrynobatrachus*. The more aquatic species *perpalmatus* eats more aquatic beetles than does the less aquatic species *natalensis*. Carabid beetles were found in 14 and *Hydrophilidae* in 16 out of 119 *perpalmatus* stomachs; the corresponding numbers of *natalensis* are 25 and 4 out of 579.

The relationship between sizes of predator and prey is complex. Generally, the intraspecific correlation between snout-vent and average volume of individual prey is low or not significant (Table 71). It reaches statistical significance in only 7 of the 20 species listed, though perhaps *Bufo funereus* and *B. melanopleura* should be added to the 7 as their coefficients approach significance ($P = 0.06$). In view of the wide snout-vent range in almost all of the species studied, one might conclude that size was not a factor in the selection of prey.

However, the *inter*specific correlation of snout-vent and volume of individual prey is high (Spearman rank coefficient +0.767) and significant ($P < 0.001$). For this correlation the medians (in Table 71) for each species were used. This strong correlation shows that prey size was a factor in food selection. Apparently each species has an inherent food size range, and an individual frog responds to prey in that range almost without regard to its own size. The inherent prey size range is probably adjusted to the average snout-vent length of adults of the particular species.

TABLE 70. — **Dominance-frequency distributions of principal prey types in the diets of amphibians in the Parc National de l'Upemba.**

« Dominance » explained in text.

	Xenopus	*Bufo*	*Rana*	*Arthroleptis*	*Phrynobatrachus*	*Kassina*	Totals	Chi-square	P
				Formicidae					
Dominant	1	20	1	3	18	0	43		
Non-dominant ...	3	0	5	0	4	1	13		
Totals	4	20	6	3	22	1	56	29.37	<0.001
				Coleoptera					
Dominant	4	20	5	1	20	1	51		
Non-dominant ...	0	0	1	2	2	0	5		
Totals	4	20	6	3	22	1	56	15.08	0.01
				Hemiptera					
Dominant	0	5	2	0	13	1	21		
Non-dominant ...	4	15	4	3	9	0	35		
Totals	4	20	6	3	22	1	56	11.58	0.05
				Isoptera					
Dominant	1	6	0	3	5	0	15		
Non-dominant ...	3	14	6	0	17	1	41		
Totals	4	20	6	3	22	1	56	11.11	0.05
				Araneida					
Dominant	0	3	5	0	3	0	11		
Non-dominant ...	4	17	1	3	19	1	45		
Totals	4	20	6	3	22	1	56	18.81	0.004

TABLE 70 *(continued.)*

	Xenopus	*Bufo*	*Rana*	*Arthro-leptis*	*Phryno-batrachus*	*Kassina*	Totals	Chi-square	P
					Orthoptera				
Dominant	1	1	3	1	0	0	6		
Non-dominant ...	3	19	3	2	22	1	50		
Totals	4	20	6	3	22	1	56	14.87	0.01
					Diptera				
Dominant	2	0	0	0	6	0	8		
Non-dominant ...	2	20	6	3	16	1	48		
Totals	4	20	6	3	22	1	56	12.19	0.04

One of the results of this type of stimulus-response relationship is that the ecological isolation of predator species is reinforced. If there were strong intra- as well as interspecific correlations, subadults of one species (e.g., ***Phrynobatrachus natalensis***) would compete with adults of a smaller species (e.g., ***P. gutturosus***). Under the circumstance observed, competition of these two species is reduced.

Some species differ in average size of food even though they have similar snout-vent ranges. For example, ***Bufo regularis*** has approximately the same size range and median as ***Rana fuscigula***, yet the average sizes of their respective prey differ (Table 71). Comparison of the average volume of individual prey in the stomachs summarized in Table 71 shows the difference between these two species to be highly significant (Mann-Whitney test : $Z = 6.00$, $P < 0.001$). This difference probably accounts for qualitative differences between the diets of these two species.

Formicidae (Table 65) are a dominant element in the diet of ***Bufo regularis*** (in 204 out of 235 stomachs) but not in that of ***Rana fuscigula*** (in 85 out of 273 stomachs). *Coleoptera* (Table 66) are eaten in large amounts by both species (in 129 stomachs of ***fuscigula***, 160 of ***regularis***), whereas *Orthoptera* occur in more stomachs of ***fuscigula*** (68) than of ***regularis*** (23). The volumes of individual prey of *Formicidae*, *Orthoptera*, and *Carabidae* (chosen as a representative, abundant family of *Coleoptera*) found in stomachs of ***Bufo regularis*** do not differ significantly from the respective volumes found in ***Rana fuscigula*** (Table 72).

TABLE 71. — **Summary of predator size and prey volume and number in 50 randomly chosen stomachs of amphibians from the Parc National de l'Upemba.**

If less than 50 stomachs were available, actual number used is in parentheses after name.

Species	Snout-vent		Total volume of prey per stomach		No. of prey organisms per stomach		Average volume of individual prey per stomach		Correlation (*) between predator snout-vent and average volume of individual prey
	Range	Median	Range	Median	Range	Median	Range	Median	
Xenopus laevis	30.7–69.6	47.0	0.001 – 4.950	0.080	1–88	3	0.001 –4.950	0.018	+0.082
Bufo regularis	42.0–99.9	59.1	0.002 –13.310	0.200	1–172	11	0.001 –0.158	0.024	—0.035
Bufo funereus	40.5–62.9	47.2	0.002 – 2.190	0.161	1–263	13	0.001 –0.213	0.014	+0.224
Bufo ushoranus (19)	20.1–25.0	23.0	0.009 – 0.434	0.079	7–128	21	0.001 –0.023	0.0025	+0.063
Bufo melanopleura (36)	16.3–25.1	21.2	0.0075– 0.189	0.055	5–129	46	0.0005–0.006	0.0013	+0.258
Rana fuscigula	40.8–97.5	56.8	0.001 – 2.340	0.240	1–23	3	0.001 –0.800	0.073	+0.187
Rana frontalis	35.0–46.7	41.9	0.001 – 0.590	0.195	1–8	2	0.001 –0.300	0.096	*+0.400*
Rana mascareniensis	36.9–56.9	43.2	0.020 – 0.840	0.150	1–12	2	0.010 –0.840	0.060	+0.072
Rana grandisonae	34.2–49.4	39.2	0.020 – 0.780	0.125	1–11	2	0.018 –0.300	0.052	*+0.294*
Rana uzungwensis (41)	31.4–45.7	35.3	0.020 – 0.900	0.100	1–8	2	0.008 –0.450	0.050	*+0.250*
Rana porosissima	31.3–52.7	40.4	0.001 – 0.680	0.102	1–10	2	0.001 –0.500	0.052	+0.031
Arthroleptis stenodactylus	16.9–36.0	28.3	0.003 – 0.810	0.103	1–66	4	0.001 –0.420	0.012	*+0.236*
Phrynobatrachus anotis	15.7–23.3	19.9	0.001 – 0.173	0.010	1–16	2	0.001 –0.057	0.003	—0.080
Phrynobatrachus cryptotis ...	15.1–21.0	17.4	0.001 – 0.106	0.013	1–25	3	0.0005–0.040	0.002	—0.168
Phrynobatrachus perpalmatus .	19.8–29.2	23.0	0.001 – 0.260	0.050	1–22	3	0.0005–0.160	0.015	—0.095
Phrynobatrachus parvulus ...	12.6–22.0	17.1	0.0001– 0.087	0.013	1–53	3	0.0001–0.020	0.003	*+0.248*
Phrynobatrachus gutturosus ...	17.4–24.6	20.5	0.001 – 0.130	0.013	1–24	4	0.0009–0.130	0.004	—0.068
Phrynobatrachus natalensis ...	26.1–37.5	30.2	0.001 – 0.502	0.073	1–154	4	0.001 –0.200	0.021	*+0.286*
Kassina senegalensis	21.8–38.7	31.1	0.010 – 0.393	0.106	1–32	3	0.004 –0.100	0.030	*+0.440*
Leptopelis bocagei (14)	40.9–63.2	51.1	0.040 – 8.276	0.260	1–35	2	0.040 –0.350	0.150	+0.075

(*) Spearman rank coefficient. Statistically significant values ($P \leq 0.05$) are in italics.

If the size of individual organisms within prey categories does not change from predator to predator, the only way two predators can differ in their respective prey sizes is by concentrating on different foods. *Rana fuscigula* eats much larger prey than *Bufo regularis;* it also eats fewer *Formicidae* (the smallest of the three types of prey considered at this point) and more *Orthoptera* (the largest type of prey) than *Bufo regularis*. Both amphibians feed primarily on terrestrial insects and both feed on land. Therefore, there is no à priori reason for expecting any of these three prey categories to be more abundant in the habitat of one predator than in that of the other. If, as seems reasonable, the prey categories are equally available to *R. fuscigula* and *B. regularis*, the qualitative differences in their diets must result from selective feeding, and the basis of selection of prey must be its size.

TABLE 72. — **Comparison of volumes (ml.) of individual prey of several categories eaten by *Bufo regularis* and *Rana fuscigula*.**

	No. of prey	Range	Median	Z (*)	P
		Carabidae			
Bufo regularis	82	0.004–1.10	0.05	—	—
Rana fuscigula	44	0.02 –0.20	0.03	0.936	0.35
		Orthoptera			
Bufo regularis	35	0.01 –0.48	0.15	—	—
Rana fuscigula	85	0.03 –1.03	0.15	0.1	>0.9
		Formicidae			
Bufo regularis	50 (**)	0.001–0.10	0.016	—	—
Rana fuscigula	12 (**)	0.001–0.08	0.014	0.28	0.76

(*) Z calculated by means of Mann-Whitney U test.

(**) Number of volume determinations in the sample of 50 randomly chosen stomachs summarized in Table 71.

Bufo regularis and *B. funereus* are both larger than the species of *Rana* (other than *fuscigula*) studied, yet the bufonids eat smaller food (Table 71). It is undoubtedly this factor that accounts for the fact that *Formicidae* are a dominant element in the diets of the two bufonids but not in those of the species of *Rana* (Table 65).

Another striking difference between the bufonids (all four species) and the other amphibians is in the number of prey organisms found in each stomach (Table 71). Only in the bufonids is the median number in excess of 10, whereas in all of the others it is below 5. The maximum number per stomach is lowest in the species of *Rana*. The large number of items in the stomachs of *Bufo regularis* and *B. funereus* is probably related to their relatively large size and the relatively small size of their prey.

The total volumes per stomach are closely related to the snout-vent lengths of the predators (interspecific correlation $+0.91$, $P < 0.001$). Given the relatively small average size of the prey of *Bufo regularis* and *B. funereus*, the only way they can achieve their total volume of food is by eating many organisms. Conversely, given the large prey size of the species of *Rana*, they need eat only a few organisms to achieve the necessary volume of food.

The small species of *Bufo* also eat numerous organisms. But as the average volume of individual prey is small, the total volumes per stomach remain proportional to the small size of the toads.

CHICAGO NATURAL HISTORY MUSEUM.

SUMMARY.

The seasonal and altitudinal distribution of the individuals studied are given separately under the appropriate species. Dominant foods, seasonal and altitudinal variation in diet, and the relation between amphibian size and prey size are discussed separately for each species.

In general, species of the genera *Bufo*, *Phrynobatrachus*, and *Arthroleptis* show the greatest degree of concentration upon a few foods. The first two genera feed heavily on *Formicidae* and *Coleoptera*, *Arthroleptis* on *Formicidae* and *Isoptera*. Thus the three most numerous groups of insects are the major sources of food for these three genera.

Species of *Rana*, *Xenopus*, and *Kassina* do not feed on *Formicidae* to the same extent as do the preceding genera. *Coleoptera* form one of the dominant prey categories in three genera. Only in *Rana* are *Araneida* and *Orthoptera* among the most important prey.

Aquatic prey (e.g., *Culicidae* larva, aquatic *Coleoptera*) are characteristic of the diet only in *Xenopus laevis*. The aquatic species, *Phrynobatrachus perpalmatus*, eats more aquatic beetles than its more terrestrial congeners, but its diet is made up largely of terrestrial arthropods. Similarly, the semiaquatic species of *Rana* feed almost wholly on terrestrial prey.

Within species, the correlation between sizes of predator and prey is usually low or non-existent, at least in the size ranges available. The interspecific correlation between sizes of predator and prey is high (+0.767). Apparently once an amphibian reaches subadult size, it responds to the entire food size range characteristic of its species.

The number of individual organisms constituting a « meal » is roughly the same for all Upemba amphibians except species of *Bufo*, which ingest almost twice as many organisms as the other species.

In general, availability determines what a given Upemba amphibian will eat. An invertebrate must be present in numbers in the habitat before it forms a significant element of a frog's diet. The small, thoroughly aquatic crustoceans (Copepoda, Ostracoda) can never form a major food source for an amphibian as terrestrial as *Arthroleptis*. Altitudinal and seasonal factors affect the availability of certain arthropods so that, for example, *Isoptera* are rarely a dominant element of the diet in the dry season and become decreasingly important with increasing altitude (Table 68).

However, selectivity, based on the size of the prey, also plays a role in determining the diet of an amphibian (Table 71).

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