INSTITUT DES PARCS NATIONAUX DU CONGO ET DU RUANDA-URUNDI

Exploration du 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

ROBERT INGER and HYMEN MARX (Chicago)

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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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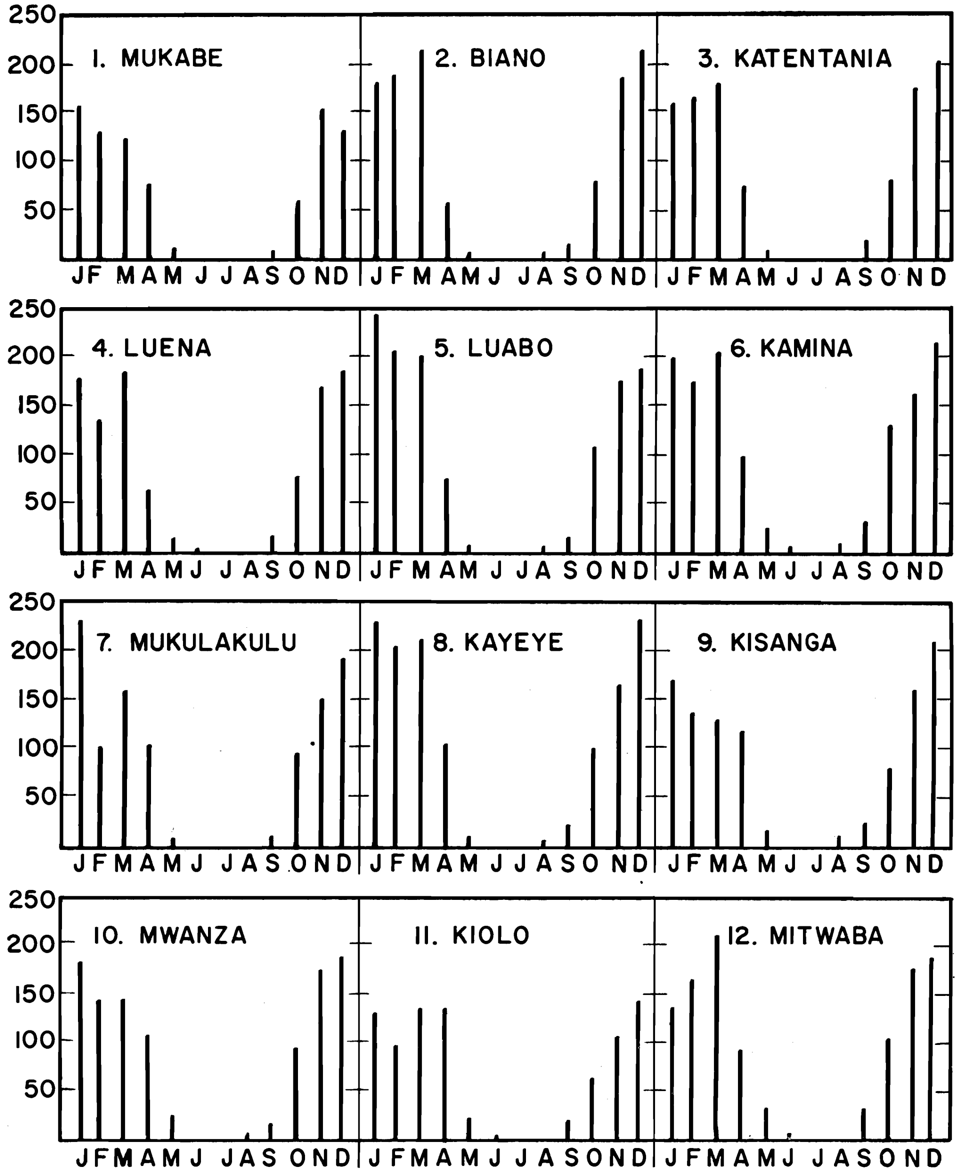

FIG. 1. — Average monthly rainfall (mm) of 12 stations surrounding the Parc National de l'Upemba.

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 *Coleptera* 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*.