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.

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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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