THE DIET OF COEXISTING SPECIES OF AMPHIBIANS IN CANADIAN JACK PINE FORESTS

M. Isabel Bellocq, Karin Kloosterman and Sandy M. Smith

Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, Ontario M5S 3B3, Canada

Diets of adults of amphibian species coexisting in the boreal forest are poorly understood. We quantified and compared the diets of adult amphibians from four jack pine (*Pinus banksiana*) forests in east-central Canada. Results showed that American toads (*Bufo americanus*) and northern redback salamanders (*Plethodon cinereus*) were predominantly ant-eaters; blue-spotted salamanders (*Ambystoma laterale*) fed mainly on snails, beetles, and insect larvae; spring peepers (*Pseudacris crucifer*) took primarily spiders and wasps; and wood frogs (*Rana sylvatica*) took a variety of alternative prey and had the highest dietary diversity. Diets of these amphibians differed significantly among the species in all study sites. Discriminant analyses showed species separation based on food type, the variable representing the proportion of ants in stomach contents being the major contributor to the discriminant functions in all assemblages.

Key words: frog, salamander, diet, feeding behaviour

INTRODUCTION

Amphibians play a key role in forest food webs, foraging on small invertebrates and serving as food to a variety of vertebrate predators (Burton & Likens, 1975; Pough *et al.*, 1987). However, amphibian ecology in general, and feeding ecology in particular, are poorly understood in boreal forest ecosystems. There is evidence that timber harvesting reduces amphibian populations (e.g. Petranka *et al.*, 1993; Dupuis *et al.*, 1995), and that habitat destruction and deforestation are factors implicated in the decline of amphibian populations worldwide (Wake, 1991). Jack pine (*Pinus banksiana*) dominates large areas of the southern boreal region in Canada and is one of the most important species in lumber and pulp production. Consequently, jack pine plantations are part of the matrix of commercially utilized forest that is subject to perturbations due to forestry practices. An understanding of the natural history and ecology of animal species inhabiting the forest is fundamental to the development of ecologically sound forest management.

Descriptions of animal diets are of general interest in natural history, and are useful for identifying food requirements of species and for understanding how animals utilize food resources. Although diets of adult amphibians have been described in both temperate (e.g. Bury & Martin, 1973) and tropical (e.g. Toft & Duellman, 1979) assemblages, most work deals with the larval stage (Wilbur, 1984 and references therein). Studies of the diets of adult amphibians, based largely on Toft's contributions (see Toft, 1985), showed that amphibians feed largely on arthropods and that species differ in their feeding strategy and degree of specialization. A very limited number of studies conducted in temperate regions suggests that frogs are opportunistic feeders (Stewart & Sandison 1972). A few studies have

reported on the diets of adults of coexisting species of amphibians in some localities within the boreal region in the Nearctic (Moore & Strickland, 1955; McAlpine & Dilworth, 1989); however, we are not aware of similar studies in jack pine forests.

Here, we quantify and compare the diets of adult American toads (*Bufo americanus*), wood frogs (*Rana sylvatica*), spring peepers (*Pseudacris crucifer*), northern redback salamanders (*Plethodon cinereus*), and blue-spotted salamanders (*Ambystoma laterale*) in four assemblages in jack pine forests. We identify their primary food and estimated the overall diet for each species. Additionally, we test whether amphibian species can be differentiated by food type in each assemblage, and identify the prey that allows separation among amphibian species based on food type.

MATERIALS AND METHODS

The study area is located in the southern boreal forest, approximately 30 km south of Gogama (47°31'N; 81°40'W), Ontario, Canada, where jack pine dominates. The area is composed of extensive monospecific forests, ranging in age from 1year to more than 60 years, as a result of artificial regeneration following clearcutting or wildfire. Mixed coniferous-deciduous forests are also present in the area. We studied the diets of adult amphibians from four jack pine forests: a 6-year old stand (Stand 1), a 35-year old stand (Stand 2), and two stands over 60 years of age (Stands 3 and 4). Different stand ages provide different assemblages of amphibians. Understory vegetation was composed of herbs and shrubs in Stand 1 and of mosses, herbs, and shrubs in Stands 2-4. Vegetation covered 64% of the ground in Stand 1, 59% in Stand 2, 71% in Stand 3, and 72% in Stand 4.

Amphibians were collected from pitfall traps during July and August 1994. These traps (one-quarter filled with water) were set to collect insects and accidentally captured amphibians as well because of their depth (ca. 20 cm). Rather than destroying valuable material, we used the latter to analyse gut contents. However, this

Correspondence: M. Bellocq, Departamento de Ciencias Biológicas, FCEN, Universidad de Buenos Aires, Ciudad Universitaria, Pab. 2, Buenos Aires 1428, Argentina.
E-mail: Bellocq@bg.fcen.uba.ar

TABLE 1. Species composition and mean head-body length (±SD) of amphibians in four jack pine forests in the southern boreal region of east-central Canada. An "x" means that the species was in the site but the number of individuals caught was not sufficient to provide a good representation of the diet. A capital "X" means that the diet of the species was described.

Species	Head-body length (cm)	Stand 1	Stand 2	Stand 3	Stand 4
Bufo americanus	1.44±0.44	X	X	X	
Rana sylvatica	2.30±0.43	X	X	x	X
Pseudacris crucifer	1.64±0.07	x	X	x	x
Rana septentrionalis		x			
Ambystoma laterale	4.69±0.81	X	X		
Plethodon cinereus	3.81±0.32	X		X	
Ambystoma maculatum		x			
Notophthalmus viridescens		x			

approach is not recommended for sampling and the use of shallower pans (ca. 5 cm) appears now to prevent such accidental captures. Amphibian abundance was not addressed in this paper because specimens found alive in the traps were set free, and that would bias any estimate. It is unlikely that captured amphibians fed while in the pitfall traps because terrestrial species search for live prey (insects usually die shortly after falling into the trap), which are unlikely to be found in the traps.

In Stand 1, pitfall traps (15 m apart) were established in two grids (approximately 500 m apart) following a 7 x 7 point pattern. They operated over six consecutive days every two to three weeks and were checked at the end of each sampling period. In Stand 2, two lines (approximately 400 m apart) of 25 traps each were established, and a single similar trap line was set in Stands 3 and 4. In Stands 2, 3, and 4, traps were checked weekly and operated continuously. Amphibians caught by pitfall traps were placed in labelled plastic bags and frozen for later dissection.

A total of eight species of amphibian was found in pitfall traps, six in Stand 1, five in Stand 2, four in Stand 3, and three in Stand 4 (Table 1). Given the number of available stomachs, we were able to describe the diet of five out of eight captured species, and for 11 out of the 18 possible species and site combinations (Table 1).

Amphibians were identified and the head-body length was measured. Stomach contents were removed and preserved in 50% alcohol, and they were analysed under the microscope. Prey items were identified to the level of Order in most cases. Larvae and adult insects were considered separate food items because their habitat, mobility, and caloric contents are usually different. Stomach contents were quantified by counting the number of individuals of each food type. Number of individuals was recorded rather than volume because we wanted to test whether amphibian species could be separated by the type of food they ate and not whether their bioenergetics differed. We took a conservative approach by estimating the minimum number of food items per stomach (Jaeger & Barnard, 1981), and only those stomachs containing three or more individual food items were considered in the analysis. We estimated the percentage frequency of each type of food

for each stomach ($\%n_i$ = number of individual items of food type i in a stomach/total number of individual food items x 100), and summarized data for each amphibian species and site as the average percentage frequency of each type of food ($\%n$). We estimated the percentage frequency of occurrence for each type of food ($\%f$) as the number of stomachs in which each food type was found over the total number of stomachs examined multiplied by 100. The cumulative frequency of new food types appearing in the diet as a function of the number of stomachs analysed indicated that three to eight stomachs were sufficient to account for most food types represented in diets for the different combinations of species and sites (Heck *et al.*, 1975). To take a conservative approach, however, a species was excluded from the analysis when fewer than five specimens were available.

Stepwise discriminant analysis (BMDP software, 7M procedure) was performed to test whether coexisting species of amphibians could be distinguished by the types of food found in their stomachs, and to identify the types of food that reflected species differences. The variables used in the multivariate analysis were the percentage frequencies of the total number of prey items found in the stomachs of individual amphibians ($\%n_i$). Larvae of Coleoptera (beetles), Lepidoptera (caterpillars), Diptera (maggots), and the unidentified insect larvae were pooled in a single food category (insect larvae). The adults of Lepidoptera (moths), Hemiptera (bugs), Homoptera (hoppers, aphids), Protura (telson tails), Thysanoptera (thrips), Myriapoda (centipedes, millipedes), and Pseudoscorpionida (false scorpions) were not included as variables because they occurred only occasionally in stomachs (representing all together 1.7%-15.5% of the average diets), and their frequency distributions did not reach normality even after data transformation. Thus, nine food type variables were considered to represent the most common food types: insect larvae (LAR), Coleoptera (COL, beetles), Diptera (DIP, flies), Formicidae (FOR, ants), Other Hymenoptera (HYM, wasps), Collembola (COLL, springtails), Acari (ACA, mites), Araneae (ARA, spiders), and Gastropoda (GAS, snails). Log- and square-root transformations were the most effective to satisfactorily normalize variable distributions.

TABLE 2. Overall average percentage frequency of the total number of prey items (% n) and percentage frequency of occurrence of prey items (% f) in stomachs of five amphibian species (*Bufo americanus, Rana sylvativa, Pseudacris crucifer, Plethodon cinereus*, and *Ambystoma laterale*) in Canadian jack pine forests. *n*: number of stomachs analysed; *H'*: Shannon-Wiener diversity index.

Prey type:	*Bufo* (n=36)		*Rana* (n=41)		*Pseudacris* (n=5)		*Plethodon* (n=43)		*Ambystoma* (n=12)	
	% n	% f	% n	% f	% n	% f	% n	% f	% n	% f
Insect larvae:										
Coleoptera	0.8	13.6	2.6	21.9	2.2	20.0	4.1	27.9	12.2	41.7
Lepidoptera	1.4	11.1	3.2	24.4	8.1	60.0	0.9	4.6	1.2	8.3
Diptera	0	0	1.3	9.7	1.7	20.0	0.3	2.3	0	0
Unidentified	1.2	25.0	3.4	21.9	0	0	3.5	27.9	8.0	33.3
Adult insects:										
Coleoptera	10.5	75.0	10.2	58.5	3.9	40.0	6.1	53.5	15.9	58.3
Lepidoptera	0.3	25.0	4.6	21.9	0	0	0.3	2.3	7.1	25.0
Diptera	4.6	58.3	10.5	63.4	17.0	100.0	2.4	27.9	9.6	58.3
Formicidae	37.9	88.9	6.6	36.6	5.3	40.0	25.7	83.7	4.5	16.7
Other Hymenoptera	13.6	88.9	15.1	82.9	25.4	100.0	10.8	60.5	7.3	41.7
Hemiptera	2.4	27.8	4.7	39.0	0	0	1.6	18.6	0.5	16.7
Homoptera	1.1	8.3	3.2	29.3	1.7	20.0	0.5	6.9	0.5	8.3
Protura	1.0	8.3	0.4	4.9	0	0	0.2	2.3	0	0
Collembola	9.6	47.2	7.3	48.8	0	0	14.7	37.2	1.3	16.7
Thysanoptera	0	0	0	0	0	0	1.0	2.3	0	0
Other arthropods:										
Myriapoda	0.3	5.6	0.2	4.9	0	0	0.3	4.6	0	0
Acarina	8.5	52.7	7.3	46.3	2.2	20.0	14.2	58.1	0.5	8.3
Araneae	4.2	55.5	13.8	73.2	30.8	100.0	8.8	48.8	5.9	33.3
Pseudoscorpionida	0.5	8.3	0.1	2.4	0	0	0.3	6.9	0.8	8.3
Other invertebrates:										
Gastropoda	2.1	27.8	5.5	46.3	1.7	20.0	4.3	53.5	24.8	66.7
Total no. of food items	745		498		49		3244		80	
H'	0.896		1.113		0.814		0.986		0.971	
Richness of food items	17		18		11		19		15	

Discriminant analysis was performed separately for each site, and species was the discriminator variable. The Shannon-Wiener index (Colwell & Futuyma, 1971) estimated dietary diversity.

RESULTS AND DISCUSSION

Most amphibian species differed in their primary food type (Table 2). Ants were the primary food of *Bufo*, occurring in 88.9% of the 36 stomachs analysed and representing 37.9% of all invertebrate food items; other prey types such as wasps and beetles were also found in toad stomachs. The diet of *Rana* showed the highest dietary diversity, in agreement with previous studies that have classified ranids as opportunistic feeders in temperate regions (Stewart & Sandison, 1972; McAlpine & Dilworth, 1989). We found that wasps, spiders, flies, and beetles were the most common prey in the stomachs of *R. sylvatica* whereas Moore & Strickland (1955) found beetles and flies to be the most common prey of this species in Alberta; differences in the consumption of primary food by *R. sylvatica* may

reflect differences in prey availability. *Pseudacris* was captured by pitfall traps in low numbers in the four study sites, and we were able to describe its diet based only on five individuals trapped in Stand 2. This species seems to feed primarily on spiders, wasps, and flies, whereas ants represented only a low proportion of the stomach contents as in *Rana*.

The two salamander species differed in the proportion of food types consumed (Table 2). We found that *A. laterale* (large size) fed mainly on snails and beetles whereas *P. cinereus* (small size) consumed primarily ants and mites. Salamanders have been identified as opportunistic feeders in which food size is more important than food type (Toft, 1985). Variations in body size among sympatric salamanders have been correlated with differences in diet (Jaeger, 1972). A study conducted by Maglia (1996) in mixed deciduous forests found that *P. cinereus* fed mainly on mites and spiders, and that the abundance of prey types in the diet differed little among populations or sites, in agreement with our findings (Table 3). *Ambystoma* had the highest percent-

TABLE 3. Average percentage frequency of the total number of individual prey items (% *n*) and percentage frequency of occurrence of prey items (% *f*) in the stomachs of amphibian species (*Bufo americanus, Rana sylvatica, Pseudacris crucifer, Plethodon cinereus,* and *Ambystoma laterale*) coexisting in four Canadian jack pine forests. *n*: number of stomachs analysed; *H'*: Shannon-Wiener diversity index.

| | Young stand | | | | Mid-age stand | | | | | |
| | *Bufo* (*n*=11) | | *Rana* (*n*=12) | | *Bufo* (*n*=5) | | *Rana* (*n*=23) | | *Pseudacris* (*n*=5) | |
Prey type:	% *n*	% *f*	% *n*	% *f*	% *n*	% *f*	% *n*	% *f*	% *n*	% *f*
Insect larvae:										
Coleoptera	0.0	0.0	4.0	25.0	0.7	20.0	2.4	17.4	2.2	20.0
Lepidoptera	0.6	9.1	3.6	33.3	0.0	0.0	2.2	17.4	8.1	60.0
Diptera	0.0	0.0	3.1	16.7	0.0	0.0	0.0	0.0	1.6	20.0
Unidentified	0.9	45.4	0.0	0.0	0.6	20.0	4.1	26.1	0.0	0.0
Adult insects:										
Coleoptera	14.6	100.0	8.8	50.0	7.9	60.0	9.5	56.5	3.9	40.0
Lepidoptera	0.0	0.0	0.0	0.0	1.5	20.0	8.0	43.5	0.0	0.0
Diptera	4.6	54.5	12.4	58.3	2.1	40.0	10.5	65.2	17.0	100.0
Formicidae	43.0	100.0	16.2	75.0	66.6	100.0	2.7	21.7	5.3	40.0
Other Hymenoptera	11.7	90.9	21.3	91.6	8.8	100.0	10.9	78.3	25.4	100.0
Hemiptera	1.4	18.2	4.6	41.7	0.5	20.0	5.1	34.8	0.0	0.0
Homoptera	0.6	9.1	4.0	25.0	0.7	20.0	2.3	21.7	1.7	20.0
Protura	0.0	0.0	0.8	8.3	0.0	0.0	0.0	0.0	0.0	0.0
Collembola	14.1	63.6	5.0	41.7	1.8	20.0	9.9	56.5	0.0	0.0
Thysanoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other arthropods:										
Myriapoda	0.8	9.1	0.0	0.0	0.0	0.0	0.1	4.3	0.0	0.0
Acarina	2.7	36.4	7.1	33.3	2.9	20.0	8.5	56.5	2.2	20.0
Araneae	2.5	54.5	7.4	50.0	2.8	40.0	15.7	78.3	30.8	100.0
Pseudoscorpionida	0.8	18.2	0.5	8.3	0.3	20.0	0.0	0.0	0.0	0.0
Other invertebrates:										
Gastropoda	0.6	9.1	1.2	16.7	3.1	40.0	8.1	60.9	1.7	20.0
Total no.of food items	216		106		138		309		49	
H'	0.770		1.030		0.589		1.079		0.812	

age of insect larvae (with 83% of the stomachs containing this food type) compared to the other amphibian species (Table 2). The primary food of this species of ambystomatid seems to be snails. When the stomachs of *A. jeffersonianum* (Jefferson's salamander) collected in deciduous forests were analysed, it was found that their diet also was comprised basically of snails and orthopterans (Judd, 1957).

Diet differed among amphibian species and ants were the main food type that was distinct among the species (Table 3). Discriminant analysis showed that coexisting individuals of *Bufo* and *Rana* differed in the type of food found in their stomachs in Stand 1 (eigenvalue=0.5341, Wilks' Lambda $F_{1,20}$=10.683, P=0.004). Most individuals (86.4% of the total cases, canonical correlation=0.590) were correctly assigned to species by the single discriminant function based on ants (variable FOR). *Bufo* (species centroid=0.7) tended to feed more and *Rana* (species centroid=-0.7) less on ants. In Stand 2, results showed significant dif-

ferences in diet among amphibian species (Wilks' Lambda $F_{8,116}$=11.237, P<0.0001) (Table 3). The first and second discriminant functions accounted for 95.3% and 4.7% of the total variance, respectively (canonical correlation of the first and second function was 0.808 and 0.292, respectively). Discriminant functions correctly classified 53.1% of the total cases to the actual species. Food type variables representing ants (FOR) and insect larvae (LAR) contributed the most to the functions (Fig. 1). Amphibian species coexisting in Stands 3 and 4 also differed in the proportion of food types found in their stomachs (Stand 3: eigenvalue=1.2865, Wilks' Lambda $F_{2,24}$=15.438, P<0.0001; Stand 4: eigenvalue=0.3377, Wilks' Lambda $F_{1,21}$=7.092, P=0.0145; Table 3). In Stand 3, 88.9% of the individuals could be correctly classified by the discriminant function as either *Bufo* or *Ambystoma* (canonical correlation=0.750). The proportion of ants and mites (variable ACA) in the diets was the major contributor to the discriminant function, in

TABLE 3 (continued...)

| Prey type: | Mid-age stand | | | | Mature stand 1 | | | | Mature stand 2 | | | |
| | Plethodon (n=26) | | Ambystoma (n=5) | | Bufo (n=20) | | Ambystoma (n=7) | | Rana (n=7) | | Plethodon (n=17) | |
	% n	% f	% n	% f	% n	% f	% n	% f	% n	% f	% n	% f
Insect larvae:												
Coleoptera	4.3	23.1	14.6	60.0	1.2	20.0	0.2	28.6	0.9	16.7	3.7	29.4
Lepidoptera	0.0	0.0	2.9	20.0	2.2	15.0	0.0	0.0	5.6	16.7	2.2	11.8
Diptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	33.3	0.8	5.9
Unidentified	3.2	30.8	5.0	20.0	1.0	15.0	10.1	92.9	7.4	50.0	4.1	23.5
Adult insects:												
Coleoptera	5.2	42.3	13.8	60.0	8.8	65.0	17.4	57.1	15.8	83.3	7.6	64.7
Lepidoptera	0.5	3.8	5.4	20.0	0.1	5.0	8.3	28.6	1.0	16.7	0.0	0.0
Diptera	2.0	30.8	9.9	60.0	5.3	65.0	9.5	57.1	6.9	66.7	3.0	23.5
Formicidae	26.4	92.3	4.0	20.0	28.0	80.0	4.8	14.3	2.4	16.7	24.6	70.6
Other Hymen.	10.1	53.8	4.7	40.0	15.8	90.0	9.2	42.9	18.7	83.3	12.0	70.6
Hemiptera	0.5	11.5	0.0	0.0	3.5	35.0	0.9	14.3	3.6	50.0	3.3	29.4
Homoptera	0.4	7.7	0.0	0.0	1.5	5.0	0.9	14.3	5.1	66.7	0.7	5.9
Protura	0.3	3.8	0.0	0.0	1.8	15.0	0.0	0.0	1.0	16.7	0.0	0.0
Collembola	17.4	46.2	1.8	20.0	9.2	45.0	0.9	14.3	1.8	33.3	10.7	23.5
Thysanoptera	1.6	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other arthropoda:												
Myriapoda	0.1	3.8	0.0	0.0	0.1	5.0	0.0	0.0	1.0	16.7	0.5	5.9
Acarina	16.8	69.2	0.0	0.0	13.1	70.0	0.9	14.3	2.2	33.3	10.2	41.2
Araneae	8.3	53.8	4.9	40.0	5.4	60.0	6.5	28.6	19.7	100.0	9.4	52.9
Pseudoscorpions	0.6	11.5	2.0	20.0	0.3	5.0	0.0	0.0	0.0	0.0	0.0	0.0
Other invertebrates:												
Gastropoda	2.4	26.9	31.0	80.0	2.6	35.0	20.4	57.1	14.2	50.0	7.2	35.3
Total no. of food items	2010		34		391		46		83		1234	
H'	0.934		0.924		0.965		0.875		1.104		1.013	

which the diet of *Bufo* (species centroid=0.65) showed a high percentage of ants and mites compared to *Ambystoma* (species centroid=-1.84). In Stand 4, ants (FOR) contributed the most to the discriminant function that correctly classified 73.9% of individuals into *Rana* or *Plethodon* (canonical correlation=0.502). *Rana* (species centroid=-0.93) showed low and *Plethodon* high (species centroid=0.33) values of the canonical variable.

The diets of some amphibian species differed among stands (Table 3). Ants comprised a higher percentage of the diet of *Bufo* in Stand 2 than in the other stands; dietary diversity of this species was also lower in Stand 2. Some differences in the proportion of food types in stomachs of *Rana* occurred between sites; the proportion of ants in the diet was lower and that of spiders higher in Stand 2 than in the other sites. The diet of *Ambystoma* was similar in Stands 2 and 3, whereas the diet of *Plethodon* was also similar in Stands 2 and 4. Differences in diet between the sites may be due to factors such as prey availability and interspecific

competition. The age of the stand creates different environmental conditions (e.g. shaded conditions, amount of woody debris) that influence insect communities and thus, food availability for insectivorous vertebrates. However, some amphibian species (e.g. *Bufo*) seem more likely to have different dietary contributions depending on the site than others (e.g. *Plethodon*), and this may be related to the individual species with which they are associated. Different amphibian assemblages also occurred at the different sites (Table 1).

Most amphibian species coexisting in jack pine stands were distinguished from each other based on the type of food they ate. However, that does not necessarily mean that they actually discriminate food by type because differences in diet may reflect differences in microhabitats. Based on her extensive review of resource partitioning in amphibians and reptiles, Toft (1985) found that 100% and 94% of the studies she reviewed demonstrated that salamanders and frogs, respectively, partitioned food resources. She also pointed out that salamanders tend to be opportunistic
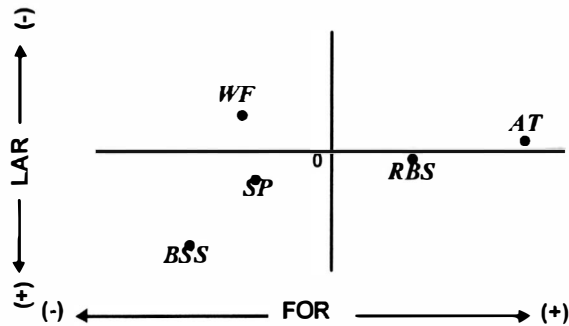
FIG. 1. Position of species centroids in the discriminant space showing differentiation among American toad (AT), wood frog (WF), redback salamander (RBS), spring peeper (SP) and blue-spotted salamander (BSS) based on food type consumed in a jack pine forest (Stand 2).

feeders that discriminate food by size, and that often the differences in prey type are those attributable to habitat. Frogs seem to partition food type more strongly than salamanders (Toft, 1985); however, they vary in size and occupy many kinds of habitat (more than salamanders do), which contribute to differences in diet among species. In eastern Canada, McAlpine & Dilworth (1989) found significant differences in prey size between sympatric *Rana clamitans* (green frog) and *R. catesbeiana* (bullfrog) but not between *R. clamitans* and *R. pipiens* (leopard frog). These authors assumed that food type would reflect the microhabitat used by ranids rather than a case of food partitioning *per se*. In our study, the primary food type differed among species except for the ant-eating *Bufo* and *Plethodon*. These two species were found coexisting in only one out of the four study sites, and - in that case - *Bufo* was present in low numbers (unpublished data). In the remaining assemblages, only one ant-eating species was represented.

ACKNOWLEDGEMENTS

REFERENCES

Burton, T. M. & Likens, G. E. (1975). Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* **56**, 1068-1080.

Bury, R. B. & Martin, M. (1973). Comparative studies on the distribution and foods of plethodontid salamanders in the redwood regions of northern California. *J. Herpetol.* **7**, 331-336.

Colwell, R. K. & Futuyma, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology* **52**, 567-576.

Dupuis, L. A., Smith, J. N. M. & Bunnell, F. (1995). Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Cons. Biol.* **9**, 645-653.

Heck, K. L., Van Belle, G. & Simberloff, D. (1975). Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* **56**, 1459-1461.

Jaeger, R. G. (1972). Food as a limited resource in competition between two species of terrestrial salamanders. *Ecology* **53**, 535-546.

Jaeger, R. G. & Barnard, D. E. (1981). Foraging tactics of a terrestrial salamander: choice of diet in structurally simple environments. *Am. Nat.* **117**, 639-664.

Judd, W. W. (1957). The food of Jefferson's salamander, *Ambystoma jeffersonianum*, in Rondeau Park, Ontario. *Ecology* **38**, 77-81.

Maglia, A. M. (1996). Ontogeny and feeding ecology of the red-backed salamander, *Plethodon cinereus*. *Copeia* **3**, 576-583.

McAlpine, D. F. & Dilworth, T. G. (1989). Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. *Can. J. Zool.* **67**, 2244-2252.

Moore, J. E. & Strickland, E. H. (1955). Further notes on the food of Alberta amphibians. *Am. Midl. Nat.* **54**, 253-256.

Petranka, J. W., Eldridge, M. E. & Haley, K.E. (1993). Effects of timber harvesting on southern Appalachian salamanders. *Cons. Biol.* **7**, 363-370.

Pough, H. F., Smith, E. M., Rhodes, D. H. & Collazo, A. (1987). The abundance of salamanders in forest stands with different histories of disturbances. *Forest Ecology and Management* **20**, 1-9.

Stewart, M. M. & Sandison, P. (1972). Comparative feeding habits of sympatric minkfrogs, bullfrogs and green frogs. *J. Herpethol.* **6**, 241-244.

Toft, C. A. (1985). Resource partitioning in amphibians and reptiles. *Copeia* **1**, 1-21.

Toft, C. A. & Duellman, W. E. (1979). Anurans of the lower Río Llullapichis, Amazonian Peru: a preliminary analysis of community structure. *Herpetologica* **35**, 71-77.

Wake, D. B. (1991). Declining amphibian populations. *Science* **253**, 860.

Wilbur, H. M. (1984). Complex life cycles and community organization in amphibians. In *A new ecology: novel approaches to interactive systems*, 195-224. Price, P. W., Slobodchikoff, C. N. and Gaud, W. S. (Eds.). NY: John Wiley and Sons.