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Prey Selectivity and Size-specific Diet Changes in *Bufo cognatus* and *B. woodhousii* during Early Postmetamorphic Ontogeny

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Ontogenetic diet shifts have been documented in many anurans (Smith and Bragg, 1949; Oplinger, 1967; Labanick, 1976; Christian, 1982; Donnelly, 1991; Lima and Moreira, 1993). These studies compared the diets of juveniles as a whole to those of adults (e.g., Livezey, 1961; Clarke, 1974a; Gittins, 1987). Diet patterns among juvenile size classes, however, have yet to be investigated. Bufonids exhibit high postmetamorphic growth rates early in ontogeny, as do other anurans (Clarke, 1974b). These differences in body size may be a means of avoiding overlap in resource use (Schoener, 1974; Toft, 1985). Hence, diet shifts associated with rapid growth during this relatively short period may be important for survival to reproductive age and may affect interactions with hetero- and conspecifics (Werner and Gilliam, 1984).

Discrete, size-specific diet shifts may result in selectivity for different prey among toad size classes (Werner and Gilliam, 1984). Some authors have suggested that certain *Bufo* feed indiscriminately (e.g., Smith and Bragg, 1949; Clarke, 1974a; Duellman and Trueb, 1986; Larsen, 1992). However, these conclusions could be an artifact of pooling size classes consisting of selective feeders into a single class for dietary analysis. Indeed, recent studies indicate that toads are selective predators (e.g., Toft, 1980, 1981). We quantified ontogenetic differences in the diets of toads over a range of sizes that occur within the first month after metamorphosis, and compared prey consumption to prey availability for several prey types consumed by juvenile toads during early ontogeny.

We collected postmetamorphic, juvenile toads by hand while walking a transect 1 m from the edge of Rose Lake, a prairie-pothole marsh located approximately 5 km NE of Vermillion, Clay Co., South Dakota. We collected 36 *Bufo cognatus* and 14 *B. woodhousii* on 15 July 1992, and 20 *B. woodhousii* on 27 July 1993. During 1992, all breeding occurred on 15–18 May and most tadpoles of *Bufo* transformed around 15 June (Graves et al., 1993). The average SVL of *B. woodhousii* at metamorphosis in South Dakota is 10 mm (Underhill, 1960). The largest toad collected had a SVL of

23.6 mm. Labanick and Schlueter (1976) indicated that this size is reached in approximately one month. Therefore, we estimated that the toads were approximately one month postmetamorphosis. The toads collected in 1993 were also estimated to be approximately one month postmetamorphosis.

We immediately placed the toads in 10% formalin and observed no regurgitation of stomach contents. In the lab, we weighed each toad to the nearest 0.01 g immediately after removal from formalin, then SVL was measured to the nearest 0.1 mm using a micrometer. We dissected each specimen and analyzed stomach contents using a dissecting microscope. We identified prey items to family (when possible) and measured total length (from anterior tip of the frons to posterior tip of the abdomen) to the nearest 0.1 mm with an ocular micrometer. Partially digested prey were identified and measured when possible.

Immediately after collecting toads in 1993, we collected 25 invertebrate samples spaced at 1 m intervals along the same transect using a gas powered D-vac (D-Vac Company, Ventura, California) for approximately 30 sec. We preserved samples in 70% ethanol, identified specimens to family when possible, and measured the length of each prey item to the nearest 0.1 mm. Electivity values for each prey category consumed by toads collected in 1993 were calculated using Jacobs' electivity index (Jacobs, 1974). Values for this index vary from 1 to -1. A value close to 1 indicates the prey type occurred often in toad diets, but was scarce in the environment. Low values indicate that the prey type was rarely found in toad stomachs, but was abundant in their environment.

Data were checked for normality and homoscedasticity. If these parametric assumptions were not met, and if transformations did not normalize the data, nonparametric statistics were used for analyses. An alpha level of 0.05 was used in all statistical tests.

Potential differences in diet between the two species collected in 1992 were investigated with the following comparisons. Toad mass, toad length, total number of prey in the stomach, and mean, maximum, and minimum prey length for each toad were compared between species using one-way ANOVA. The proportion of each prey category in the diet was compared between the two species using Kruskal-Wallis ANOVA. The relationship between toad size and prey size was compared between species using analysis of covariance. There were no significant differences between the diets of the two toad species collected in 1992 in any of the comparisons made. Therefore, data from the two species were pooled for all subsequent analysis.

Relationships between 1992 toad mass and mean, minimum, and maximum prey length were investigated using regression analysis. The percent of stomach contents represented by the number of prey in each category was arc-sine transformed and regressed against toad mass.

Because 1993 toads were significantly smaller than 1992 toads ($t = 2.098$, $P = 0.04$), only 1992 toads whose mass was <0.8 g (the mean mass of toads in 1992) were used to compare diets between years. Thus, masses of the two groups were not significantly dif-

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ferent ($t = -0.191$, $P = 0.85$). The frequency of each prey type in toad stomachs was compared between these samples of toads collected in 1992 and 1993 using Chi-square tests.

Toads collected in 1992 ranged in length from 10.5 to 23.6 mm, and in mass from 0.16 to 1.68 g. Prey lengths ranged from 0.7 to 4.7 mm. The number of prey in a stomach ranged from 0 to 62. All identifiable prey were arthropods. These were grouped into nine categories, including six insect orders, spiders, mites, and unidentified larvae (Table 1).

Toad mass was positively correlated with mean, minimum, and maximum prey length ($P < 0.001$ for all prey lengths; Fig. 1). Toad mass and the number of prey in toad stomachs were not significantly correlated (Spearman rank correlation: $r_{50} = -0.14$; $P = 0.34$). Smaller toads consumed larger proportions of collembolans ($R^2_{1,48} = 0.27$; $P < 0.001$; Fig. 2A) and mites ($R^2_{1,48} = 0.08$; $P < 0.05$; Fig. 2B), while coleopterans made up greater proportions of the diet in large toads ($R^2_{1,48} = 0.45$; $P < 0.0001$; Fig. 2C). Proportions of other prey types did not vary with individual size.

Toads collected in 1993 ranged in length from 12.1 to 26.4 mm, and in mass from 0.2 to 2.4 g. Coleopterans were consumed by all toads and occurred with the highest frequency (Table 1). Electivity indices suggest that juveniles specialized on beetles, which were scarce in the environment, and avoided collembolans, which were abundant in the environment. No unknown larvae were found in the D-vac prey samples. There-

TABLE 1. Percent of total diet represented by each prey category and percent of toad stomachs containing that taxa from juvenile *Bufo cognatus* and *B. woodhousii* collected in 1992 and *B. woodhousii* collected in 1993. Data from both 1992 toad species were pooled after no significant differences were found. Electivity index values for prey categories from 1993 were calculated as by Jacobs (1974). Specific data on the families of prey consumed will be provided by the authors upon request.

Prey type	Percent of total diet		Percent of stomachs		Electivity index (1993)
	1992	1993	1992	1993	
Acarina	3.3	7.9	22	70	0.54
Araneae	1.6	7.7	26	60	0.18
Collembola	43.0	3.8	68	45	-0.95
Homoptera	1.9	8.1	24	75	-0.03
Hemiptera	4.1	1.4	26	25	-0.07
Coleoptera	25.7	57.6	90	100	0.94
Diptera	9.2	3.4	66	55	-0.62
Hymenoptera	2.8	5.1	30	65	0.62
Unknown	5.8	4.8	44	60	1.00
Unidentifiable prey	3.5	—	18	—	—

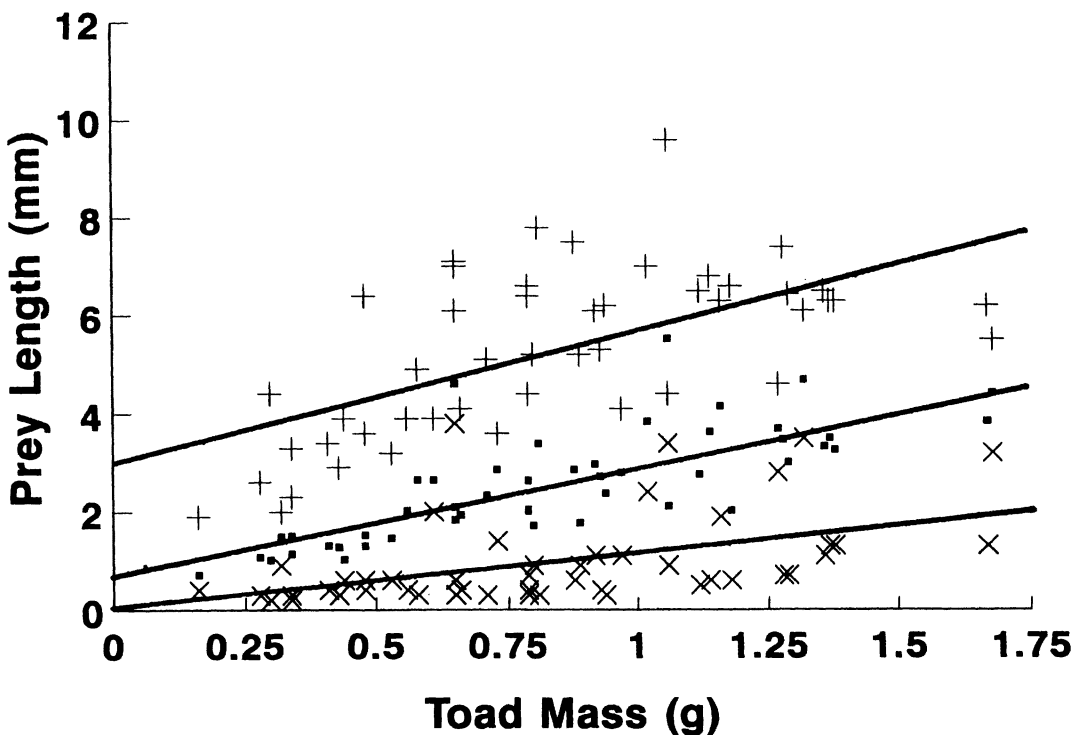


FIG. 1. Relationship between toad mass and mean prey length (■), maximum prey length (+), and minimum prey length (×) for juvenile *Bufo cognatus* and *B. woodhousii* collected in 1992 ($N = 50$). Lines show least squares regressions with equations of $y = 2.27x + 0.65$ (mean), $y = 2.81x + 2.91$ (maximum), and $y = 1.19x - 0.00$ (minimum).

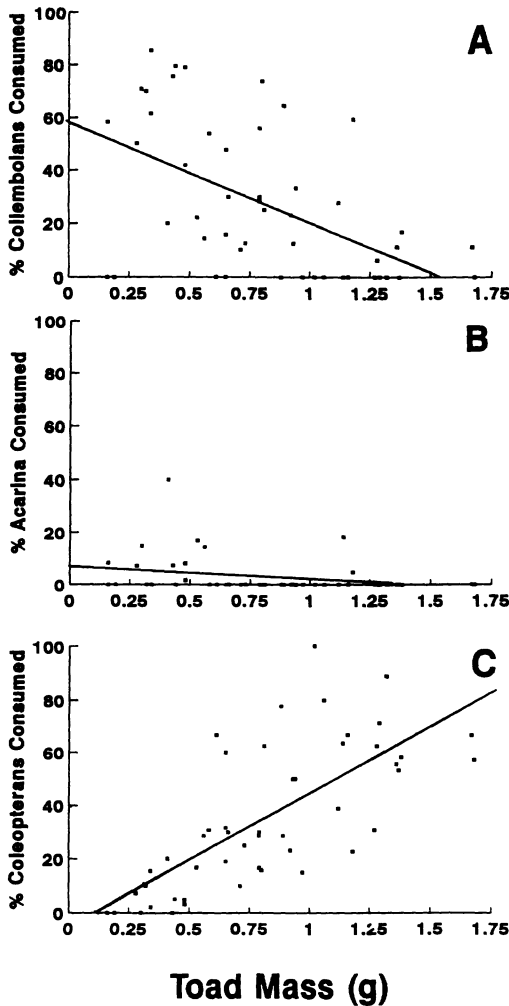


FIG. 2. Relationship between body mass and percent of stomach contents represented by A) collembolans, B) mites, and C) coleopterans for juvenile *Bufo cognatus* and *B. woodhousii* collected in 1992 ($N = 50$). The least squares regression equations are A) $y = -37.21x + 57.69$, B) $y = -5.21x + 7.03$, and C) $y = 51.11x - 5.82$.

fore, though these prey were rarely consumed, their apparent absence from the habitat samples produced a high selectivity value. We believe this reflects a sampling artifact rather than selectivity by the toads. Similarly, the low index value for dipterans may be the result of sampling bias. Because the D-vac could potentially sample prey from a vertical plane (in the air) as well as horizontally (on the ground where toads would forage), dipterans would be overrepresented in the habitat samples. Hymenopterans and mites had high index values while all other prey types had index values indicating that toads consumed them in direct proportion to their abundance in the environment (Table 1). These prey types were minor components of the diet.

Chi-square tests indicated that the frequency of prey

types consumed differed significantly among years for most prey (Fig. 3). Toads collected in 1992 had significantly higher proportions of collembolans, dipterans, and hemipterans (relative to the total number of prey consumed), and significantly fewer coleopterans, mites, spiders, homopterans, and hymenopterans in their diets than toads collected in 1993.

Although toads from the 1993 sample consumed few collembolans, those that were eaten were significantly larger than in 1992 ($P < 0.01$) and significantly larger than those in the environment ($P < 0.001$). Additionally, toads in 1993 consumed significantly smaller coleopterans than in 1992 ($P < 0.001$), while coleopterans in the diet were significantly smaller than those in the environment ($P < 0.001$).

In 1992, we observed size-specific differences in diet. These differences occurred earlier in ontogeny than revealed in studies that have only contrasted juvenile and adult stages (Smith and Bragg, 1949; Livezey, 1961; Clarke, 1974a; Donnelly, 1991; Lima and Moreira, 1993). Consequently, many more changes in diet may occur during ontogeny than previously realized. One explanation for these differences is that toads are gape-limited predators. Donnelly (1991) suggested that ontogenetic changes in *Dendrobates pumilio* diet are due to gape limitations. These changes may have important effects on species interactions and community structure (Werner and Gilliam, 1984).

Electivity index values suggest that toads collected in 1993 were selective predators, contrasting with the traditional view of toads as generalist foragers. This conclusion is similar to Toft's (1981) for Panamanian bufonids. However, the toads in her sample specialized on ants, rather than beetles. Toft's (1980, 1981) conclusion that toads are active foragers is also supported by our data. According to Toft (1981) and Donnelly (1991), there may be a correlation between an active foraging strategy and the occurrence of prey that is difficult to digest in the diet (e.g., chitinous or noxious prey). This is characteristic of the beetles and mites that toads in our study preferred. Additionally, coleopterans were scarce in the environment and an active foraging strategy should result in frequent encounters with this type of prey (Huey and Pianka, 1981; Toft, 1981). Hymenopteran and mite electivity values indicate the toads preferred these prey types, although such prey made up a small portion of the toads diet. The inclusion of these prey may result from toads responding to fluctuations in prey abundance (Donnelly, 1991) or the toads' need to balance nutrients in their diet (Clark, 1982).

There was a distinct difference in diet between similar-sized toads in the 1993 and 1992 samples. Possible mechanisms for this disparity include differences in climate and competition; 1993 was cooler and wetter during summer (SDSU Southeast Research Farm, Centerville, South Dakota) and juvenile toad density appeared much lower (personal observations).

Our results from 1992 are similar to those of Lima and Moreira (1993) and Gittins (1987) who reported that both juvenile *Colostethus stephensi* (Lima and Moreira, 1993) and juvenile *B. bufo* (Gittins, 1987) specialize on collembolans and mites. While Simon and Toft (1991) stressed the importance of mites in juvenile diets of many taxa, collembolans may also be an abundant, low-cost prey commonly utilized by anurans. However, in contrast to previous studies, we

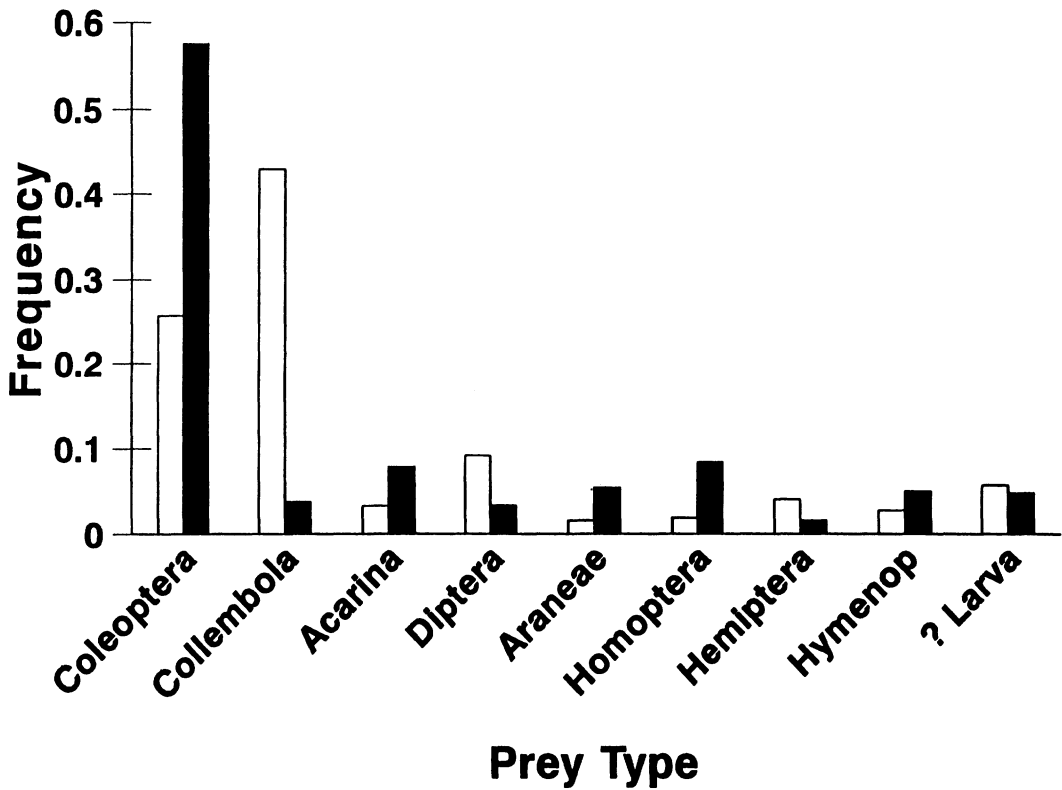


FIG. 3. Frequency of each major prey type consumed by juvenile *Bufo cognatus* and *B. woodhousii* collected in 1992 ($N = 50$) and juvenile *B. woodhousii* collected in 1993 ($N = 20$). Closed bars represent 1993 and open bars represent 1992. Frequencies of all prey types except unknown larvae were significantly different between years.

found that juvenile toads specialized on coleopterans in 1993, rather than collembolans and mites. This change in diet between years suggests that fluctuations in prey populations and toad responses to such changes should be studied for a clearer understanding of the feeding ecology of this ontogenetic stage.

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Timing of Reproduction and Metamorphosis in the Carolina Gopher Frog (*Rana capito capito*) in South Carolina

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Because of recent concerns about the status of amphibian populations (Pechmann and Wilbur, 1994), any information on life history traits related to reproduction and juvenile recruitment can become crucial in making conservation decisions. This is especially true for the gopher frog, *Rana capito*, whose life history and population status is unknown in most parts of its range (Altig and Lohoefer, 1983). State

surveys of herpetofauna have listed this species as uncommon, rare, or endangered for at least two decades (e.g., Mount, 1975; Martof et al., 1980; Dundee and Rossman, 1989; Johnson, 1987). At least two states, and perhaps others, have classified the species as threatened (e.g., in Florida by Moler, 1992; and in Alabama by Mount, 1986). During 1993 in South Carolina, verification of the presence of this species to the state's Heritage Trust Program was limited to a single observation (S. H. Bennett, pers. comm.). Its secretive nature, short breeding season, and small, patchy population distribution have all contributed to the lack of basic life history information about this anuran.

In an effort to increase our knowledge of this species, we have compiled data collected on activity patterns over the past 25 yr, including the timing of reproduction and metamorphosis of juveniles from various breeding sites on the Savannah River Site (SRS) in the Upper Atlantic Coastal Plain of South Carolina. A thorough description of the region, climate, and breeding sites mentioned in this report is given by Gibbons and Semlitsch (1991) or cited therein.

Rana capito adults have been collected at only seven (27%) of the ponds and Carolina bays effectively sampled on the SRS (41 sampling years). They have never been collected or heard at any large aquatic habitats such as the man-made reservoir system of PAR Pond or at very ephemeral sites such as shallow roadside ditches and small borrow pits where other anuran species are often found (e.g., *Scaphiopus holbrookii*, *Bufo quercicus*). At breeding sites where they have been found, fewer than 10 adults have been collected in any year, despite continuous monitoring with drift fences and pitfall traps at these sites for multiple years as well as periodic night visits for visual and auditory observations (Table 1). In addition, their frequency of breeding among years at four well-studied sites is very low (Ellenton Bay 0.30, Rainbow Bay 0.06, Karen's Pond 0.67, and Risher Pond 0.40). Finally, we have observed no apparent change in these low frequencies of breeding or small population sizes over the past 25 yr.

The breeding season in most years lasted only a few days, and occurred between January and April. In 1982 at Flamingo Bay, the breeding season was more protracted and adults were found entering the site during two distinct periods, mid-February and again in mid-March. This was also observed at Karen's Pond in 1970 where one adult was found entering the pond as late as 2 April. The body size of collected adults ranged from 59.0–91.0 mm snout-vent length (\bar{x} = 76.1 \pm 10.32 mm SVL, N = 21; Table 1).

Metamorphosing juveniles were seldom found at sites, and they were even less frequent than the occurrence of breeding adults alone would suggest. During one year, emigrating juveniles (N = 50) were found in pitfall traps at the drift fence at Karen's Pond between 21 June and 10 July 1970 and averaged 36.7 \pm 1.8 mm SVL. Metamorphosing juveniles (N = 46) were collected at a series of partial drift fences near Pond C between 18 June and 28 July 1971 (\bar{x} = 41.0 \pm 2.9 mm SVL). Also, metamorphosing juveniles were first captured emigrating from Flamingo Bay on 27 May 1982 and continued to leave through 12 July. In total, 25 metamorphs were captured leaving during