Diet Composition in Postmetamorphic Bullfrogs and Green Frogs: Implications for Interspecific Predation and Competition

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ABSTRACT. – We examined diet composition of postmetamorphic bullfrogs (Rana catesbeiana) and green frogs (R. clamitans) co-occurring at two study sites in southwest Michigan to gain insight into the nature of potential interactions between the species. Observations during sample collection indicated that bullfrogs tended to be found in the water and green frogs tended to be on land within a few meters of the water’s edge. This habitat difference was reflected in diet composition. The percentage of the diet composed of aquatic prey items was significantly higher for bullfrogs on three of four collection dates. Comparisons of adult and juvenile classes of the two species indicated interspecific diet similarity was negatively related to the body size difference between classes. Juvenile frogs were common in the diet of adult bullfrogs, but were almost never consumed by green frogs. The small size of frogs consumed by adult bullfrogs indicated that juvenile green frogs constituted the great majority of frogs eaten. Our results suggest that, because of differences in habitat and body size, the opportunity for substantial competition between these species is probably small, and is restricted to individuals of similar body size. The potential for predatory interactions, however, may be substantial, and is highly asymmetrical, with the interaction largely restricted to adult bullfrogs preying on juvenile green frogs.

The majority of the world’s animal fauna has complex life cycles, or undergo marked ontogenetic shifts in niche which approximate complex life cycles (Werner, 1988). As a consequence, the ecological interactions between species in a community may be limited to a particular stage and habitat, or occur in several different life history stages but in qualitatively different form. For example, it is not uncommon in aquatic communities for two species to interact as competitors during one stage of the life cycle, but as predator and prey during another stage (Werner and Gilliam, 1984). Some amphibians are potentially archetypal examples of these sorts of interactions. In many species it is possible that both larval and transformed stages compete, but the interaction may be of quite different character in the aquatic and terrestrial stages. In other species, such as those studied here, species may interact as competitors in the larval stage but as predator and prey in the postmetamorphic stages, or the interaction may be mixed in the terrestrial stage. In general, interactions between amphibian species have been much better studied in the larval stage than in the terrestrial stage (e.g., Wilbur, 1980, 1984). In order to understand patterns of coexistence of amphibian species in time and space, it is critical to understand the concatenation of larval and adult interactions.

This study examines the diets of coexisting postmetamorphic bullfrogs (Rana catesbeiana) and green frogs (R. clamitans) and provides insight into the nature of potential interspecific interactions during the terrestrial stage. The study was conducted in the context of a broader investigation of factors responsible for the difference in distribution of the two species along an environmental gradient from permanent to temporary ponds. During the larval phase, changes in the relative success of these species along the environmental gradient arise from both competitive interactions and the changing suite of predators along the gradient (Werner, 1994; Werner and McPeek, 1994). This study suggests that predator-prey and, to a lesser degree, competitive interactions between the species may contribute to their relative success in the terrestrial phase of their life cycle.

BACKGROUND

The bullfrog is the largest North American frog, commonly reaching a size of 180–200 mm snout–vent length (SVL). The green frog is substantially smaller, typically attaining a maximum size of 95–100 mm SVL. Additionally, average bullfrog metamorphic size (46 mm SVL; Collins, 1979) exceeds that of green frogs (32 mm SVL; Martof, 1956).

Distributional surveys of the two species (Collins and Wilbur, 1979; Dale et al., 1985) indicate that on a gradient from large permanent lakes to small temporary ponds, the bullfrog’s distribution is skewed to larger permanent wa-
Table 1. Composition of samples collected for diet analysis. Snout-vent length (mean ± 1 SD) is listed for each sample date. The number of individuals collected is given in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Turkey Marsh</th>
<th>Manning Marsh</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>19 June*</td>
<td>21 July</td>
</tr>
<tr>
<td>Bullfrogs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>63.5 ± 13.1 (6)</td>
<td>58.8 ± 7.2 (13)</td>
</tr>
<tr>
<td>Adult males</td>
<td>114.9 ± 4.7 (8)</td>
<td>121.0 ± 6.0 (25)</td>
</tr>
<tr>
<td>Adult females</td>
<td>116.1 ± 13.8 (11)</td>
<td>121.7 ± 15.2 (9)</td>
</tr>
<tr>
<td>Green frogs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>39.0 ± 4.6 (21)</td>
<td>40.8 ± 7.6 (21)</td>
</tr>
<tr>
<td>Adult males</td>
<td>71.5 ± 6.3 (15)</td>
<td>73.6 ± 5.2 (39)</td>
</tr>
<tr>
<td>Adult females</td>
<td>73.7 ± 8.6 (10)</td>
<td>76.4 ± 6.0 (11)</td>
</tr>
</tbody>
</table>

* Includes individuals from a supplementary sample made on 28 June.

ners. The green frog’s distribution completely overlaps the bullfrog’s, but is broader and includes more temporary waters. Further, there is some suggestion that the green frog is more successful on regions of the gradient not occupied by the bullfrog (Collins and Wilbur, 1979; M. Stewart pers. comm.).

Factors affecting relative success of the species during the larval phase contribute to the dominance of bullfrogs in permanent habitats and green frogs in temporary or fishless habitats (Werner and McPeek, 1994). Bullfrogs are less vulnerable to fish predators than green frogs (because of skin repellents) and green frogs are less vulnerable to invertebrate and salamander predators (because they are less active). Further, because fish have strong negative effects on invertebrate and salamander predators, they indirectly facilitate bullfrog populations through the food web (Werner and McPeek, 1994). The two species also are strong competitors in the larval phase, and it appears that the bullfrog is the better competitor (Werner, 1991, 1994). Additionally, the bullfrog’s somewhat longer larval phase (Werner, 1991) restricts its distribution to the most permanent habitats. In this study we ask if interactions in the terrestrial phase would reinforce or oppose those operating in the larval phase with regard to relative success on the gradient.

Materials and Methods
We collected postmetamorphic bullfrogs and green frogs for stomach analyses from two marshes during the summer of 1987. The primary study site was Turkey Marsh, located just east of the Kellogg Biological Station in Kalamazoo County, Michigan. Turkey Marsh has a surface area of approximately 3 ha and a maximum depth of 2.5 m. It has extensive areas of submersed vegetation (primarily Chara) and an overstory of lily pads (Nuphar). We collected frogs on three sample dates separated by approximately 30 d (Table 1). To determine whether patterns observed in Turkey Marsh were specific to that habitat or applied more generally, we obtained a sample of frogs from a second habitat, Manning Road Marsh, located in Barry County, Michigan (Table 1). This habitat is larger but otherwise similar to Turkey Marsh.

We collected frogs between dusk and about 0200 h with the aid of headlamps. Frogs were captured by hand or with a dipnet, killed, and put on ice to retard digestion. Because we were interested in the role of body size in potential interactions, we collected frogs across the natural size range. Immediately upon returning to the laboratory we determined length (mm SVL), weight (the nearest 0.5 g), and sex (from examination of the gonads) of frogs, then preserved the animals in 10% buffered formalin.

Prey Items.—We classified prey items by taxon (usually at the level of family) and life stage. Additionally, we classified each prey type as either aquatic or terrestrial depending on the habitat in which it typically occurs. Ambiguous items that occur in both aquatic and terrestrial habitats were not included in analyses of prey habitat type.

For most prey items we determined prey volume as \( V = \frac{4}{3}\pi r^3 \), with prey length, \( l \), and radius, \( r \), measured to the nearest 0.16 mm with an ocular micrometer. For frogs recovered from stomachs we determined volume from a regression of frog volume (measured by fluid displacement) on femur length derived from a sample of juvenile green frogs. Femur length was used because this dimension could be reliably obtained from the stomach samples.

Data Analysis.—Overall, 87% of frogs collected contained at least one prey item, and only these individuals were used in the diet analyses. We examined patterns of diet similarity (Schaeffer, 1970) between all pairwise combinations of adult (>90 mm SVL) and juvenile bullfrogs.
and adult (>60 mm SVL) and juvenile green frogs. We tested for species differences in the use of aquatic and terrestrial items with the Mann-Whitney U-test, using the percentage of aquatic items in the diet as the test variable. To determine whether use of aquatic items depends on frog body size, we regressed the percent of diet composed of aquatic items (arc sine transformed) on frog body size (ln-transformed). We also evaluated species differences and patterns of size-dependence in (1) number of items eaten, (2) mean size of prey items, and (3) total diet volume. We examined species differences using either analysis of variance or analysis of covariance (with frog body size as the covariate), depending on whether the variable depended significantly on body size. Because adult bullfrogs were substantially larger than green frogs (e.g., mean adult mass of bullfrogs was 4.0 fold greater than that for green frogs), we restricted our tests for species differences to the size range in which the species overlapped (i.e., individuals <100 mm SVL). We combined data from the three sample dates in Turkey Marsh for these analyses. Finally, we tested for diet differences between adult males and females of each species since previous studies have indicated that sexes sometimes differ in both habitat use and diet during the breeding season (Lamb, 1984).

RESULTS

Habitat Distribution of Species.—We found marked differences in species distributions on most collection dates. Bullfrogs were almost always found floating on the water, sitting on lily pads, or in shallow water near the shore. Though a number of green frogs were also collected in the water, a substantial fraction were found on the shore, most within several meters of the water’s edge. In the Manning Road Marsh collection, for example, all but three of the larger green frogs were collected on the shore, and small green frogs (recently metamorphosed) were collected in the water. By contrast, only one bullfrog was collected on the shore. The late August collection from Turkey Marsh, however, was on a very cool evening and all the frogs collected came from the water, though green frogs were all collected within about 5 m of the shore whereas bullfrogs were distributed across the marsh surface.

Diet Composition, Specialization, and Overlap.—Although both bullfrogs and green frogs utilized a broad range of prey taxa, a few prey types tended to dominate diet composition, and, these tended to differ between frog species (Table 2). For bullfrogs the most important diet items (by diet volume) overall were juvenile frogs, aquatic Hemiptera, and adult odonates. In contrast, the major diet items for green frogs were adult beetles, wasps and bees, and arachnids. In addition to these items, adult flies and earthworms were important prey for green frogs in Manning Road Marsh.

Juvenile frogs were the largest diet items and were common in adult bullfrog diets, but were almost never consumed by green frogs. In Turkey Marsh, 39% of adult bullfrogs contained a juvenile frog compared to 1% of adult green frogs. In Manning Road Marsh 50% of adult bullfrogs contained a juvenile frog compared to 0% of green frogs. Of the frogs that consumed frogs in Turkey Marsh, 90% were larger than the largest green frog in the samples (91 mm SVL); thus size constraints may have precluded most green frogs from consuming frogs.

Bullfrogs and green frogs in both study sites generally differed in the fraction of aquatic versus terrestrial prey items (Table 2). Aquatic prey items constituted a significantly greater proportion of bullfrog diets than green frog diets ($P < 0.001$) in Manning Road Marsh and in Turkey Marsh in July and August. The exception to this pattern was the June sample from Turkey Marsh where green frogs consumed an unusually high proportion of aquatic items (Table 2). The percent aquatic items in the diet did not depend on frog size in either species ($P > 0.05$ for all samples).

Diet similarity trends suggest that the extent of diet overlap depends on life history stage (adults and juveniles) and species (Fig. 1). Similarity between conspecific classes was higher than that observed between interspecific classes and interspecific diet similarity was closely tied to differences in body size between classes. In general, interspecific diet similarity declined with increasing disparity in body size.

Number, Size, and Total Volume of Diet Items.—The number of prey items was generally independent of frog body size, though there was a weak negative relationship between these variables for bullfrogs in Turkey Marsh ($r^2 = 0.06, P = 0.01$). For frogs <100 mm SVL, the number of prey items was independent of frog size ($P > 0.10$ in all cases). The number of prey eaten did not differ between green frogs (mean ± SE = 5.5 ± 0.4) and bullfrogs (4.7 ± 0.3) in Turkey Marsh ($F_{1,166} = 0.02; P = 0.88$), but green frogs (4.3 ± 0.9) consumed more prey items than did bullfrogs (3.1 ± 0.5) in Manning Road Marsh ($F_{1,38} = 7.44; P = 0.01$).

The mean size of prey items in bullfrog and green frog diets was positively related to body size for both species in both habitats (Fig. 2). For frogs <100 mm SVL, bullfrogs consumed significantly larger items than did green frogs in both Turkey Marsh ($F_{1,165} = 9.52; P = 0.002$).
Table 2. Percentage of bullfrog and green frog diet items and volume (in parentheses) in each prey category for each study site and sample date. Though prey were usually identified to family and life stage, we present a collapsed data set for ease of presentation. Prey habitat types are: A = aquatic, T = terrestrial, ? = ambiguous. Percentage (mean ± 1 SD) of aquatic prey items in diet is also listed.

<table>
<thead>
<tr>
<th>Prey category</th>
<th>Habitat</th>
<th>Bullfrog</th>
<th>Green frog</th>
<th>Manning</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>July</td>
<td>August</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>T</td>
<td>2.3 (0.6)</td>
<td>6.5 (4.1)</td>
<td>4.4 (2.6)</td>
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<tr>
<td>Wasps and bees</td>
<td>T</td>
<td>1.1 (0.8)</td>
<td>1.6 (0.6)</td>
<td>4.7 (6.5)</td>
</tr>
<tr>
<td>Ants</td>
<td>T</td>
<td>0 (0)</td>
<td>3.5 (2.1)</td>
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</tr>
<tr>
<td>Homoptera</td>
<td>T</td>
<td>6.3 (1.2)</td>
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<td>2.3 (0)</td>
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<tr>
<td>Odonata</td>
<td>T</td>
<td>14.6 (6.7)</td>
<td>17.5 (24.1)</td>
<td>12.4 (12.9)</td>
</tr>
<tr>
<td>Larval Lepidoptera</td>
<td>T</td>
<td>2.1 (0.3)</td>
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<td>1.1 (0)</td>
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<tr>
<td>Diptera</td>
<td>T</td>
<td>10.5 (6.7)</td>
<td>3.7 (1.2)</td>
<td>5.2 (3.7)</td>
</tr>
<tr>
<td>Arachnids</td>
<td>T</td>
<td>0 (0)</td>
<td>1.5 (0.5)</td>
<td>3.2 (1.3)</td>
</tr>
<tr>
<td>Annelids</td>
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<td>0 (0)</td>
<td>0.9 (1.5)</td>
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<tr>
<td>Miscellaneous</td>
<td>T</td>
<td>10.5 (11.9)</td>
<td>11.1 (3.2)</td>
<td>11.0 (6.0)</td>
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<tr>
<td>Hemiptera</td>
<td>A</td>
<td>19.2 (18.4)</td>
<td>22.7 (15.2)</td>
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<tr>
<td>Larval Odonata</td>
<td>A</td>
<td>5.0 (5.4)</td>
<td>3.4 (3.8)</td>
<td>4.6 (5.0)</td>
</tr>
<tr>
<td>Larval Diptera</td>
<td>A</td>
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<td>7.2 (8.3)</td>
</tr>
<tr>
<td>Miscellaneous</td>
<td>A</td>
<td>1.9 (0.6)</td>
<td>7.4 (7.1)</td>
<td>6.9 (6.2)</td>
</tr>
<tr>
<td>Frogs</td>
<td>?</td>
<td>14.5 (41.3)</td>
<td>6.4 (22.7)</td>
<td>5.1 (15.1)</td>
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<tr>
<td>Metamorphosingodonates</td>
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<td>5.7 (6.5)</td>
<td>0.7 (1.0)</td>
</tr>
<tr>
<td>Miscellaneous</td>
<td>?</td>
<td>7.3 (5.2)</td>
<td>1.8 (0.6)</td>
<td>7.0 (9.0)</td>
</tr>
<tr>
<td>Sample size</td>
<td></td>
<td>23</td>
<td>46</td>
<td>45</td>
</tr>
<tr>
<td>% aquatic prey in diet</td>
<td>39.2 ± 34.4</td>
<td>45.9 ± 28.8</td>
<td>48.5 ± 34.4</td>
<td>36.3 ± 32.9</td>
</tr>
</tbody>
</table>
in both habitats (Fig. 3). For frogs <100 mm SVL, bullfrogs had greater diet volumes than green frogs in Turkey Marsh ($F_{1,166} = 6.97; P = 0.009$), but species did not differ in Manning Road Marsh ($F_{1,35} = 1.87; P = 0.18$).

**Do Sexes Differ in Diet Composition?**—Sexes did not differ in the proportion of aquatic items in the diet overall or on any sample date for either species ($P > 0.05$). There was a high degree of diet overlap between sexes in both bullfrogs (similarity = 0.723) and green frogs (similarity = 0.786).

**Discussion**

Three strong patterns that may shed light on the nature of potential interactions between bullfrogs and green frogs were evident in the diet analysis. First, in a reflection of observed differences in habitat distribution, bullfrogs relied more heavily on aquatic prey than did green frogs. Second, overlap between the species in diet resources declined with increasing body size disparity. Third, juvenile frogs were a major component of the diet of bullfrogs but not green frogs.

Our results parallel those of two other studies that have compared diets of sympatric bullfrogs and green frogs, suggesting that our results reflect general patterns in the species. These studies showed that bullfrogs tended to use aquatic habitats more commonly than green frogs (Stewart and Sandison, 1972; McAlpine and Dilworth, 1989), and accordingly the proportion of the diet composed of aquatic prey was greater for bullfrogs than green frogs (Stewart and Sandison, 1972). Additionally, small frogs were an important diet component for bullfrogs. Small *Rana* remains constituted the greatest volume and were the most numerous prey item in the diet of bullfrogs in Stewart and Sandison (1972) and were found in 59% of bullfrog stomachs in McAlpine and Dilworth (1989).

Numerous studies examining only bullfrog or green frog food habits corroborate these general patterns. These studies demonstrate both that aquatic prey constitute a substantial portion of the bullfrog diet (Surface, 1913; Munz, 1920; Korschgen, 1955; Korschgen and Basket, 1963; Fulk and Whitaker, 1968; Taylor and Michael, 1972; McCamie and Heidt, 1974), and other frogs, particularly ranids, are a very important component of bullfrog diets (Korschgen, 1955; Lewis, 1962; Brooks, 1964; Taylor and Michael, 1972; McCamie and Heidt, 1974; Corse and Metter, 1980). The few studies available on green frog diets illustrate a decided terrestrial bias in their food. For example, Hamilton (1948) found that Coleoptera, Diptera, Orthoptera, and caterpillars dominated green frog diet volume.

We suggest that the potential strength of competitive interactions between the species is

and Manning Road Marsh ($F_{1,35} = 6.75; P = 0.013$; Fig. 2).

The total volume of diet items generally increased with frog body size for both frog species.
**Fig. 2.** Mean prey size as a function of frog body size for bullfrogs and green frogs in Turkey Marsh and Manning Road Marsh. Mean prey size is significantly related to snout-vent length for both species in both habitats (Kendall's rank correlation, $P < 0.05$ for each relationship). For clarity, least square regression lines are shown for each species.

likely to be mitigated by the habitat-related diet differences. We found that bullfrogs tend to occupy aquatic habitats and often consume aquatic prey, whereas green frogs occupy terrestrial habitats around the water's edge and consume primarily terrestrial prey. The one date when diet differences did not exist was the June date in Turkey Marsh. This collection occurred dur-
ing the height of the breeding season for these species. When breeding, the green frog, especially males, spend a considerable amount of time in the water calling and it is likely that the increased fraction of aquatic prey during this period is a consequence of breeding behavior.

Body size relationships within and between species are also likely to influence the nature and strength of interactions (Fig. 1). Within species, the average size difference between juveniles and adults (about 60 and 40 mm SVL in bullfrogs and green frogs respectively) was associated with a 40% to 65% difference in diet composition. Because the proportion of aquatic items in the diet did not differ between adults and juveniles within species, much of this diet difference may be due to differences in the range of prey sizes consumed (Fig. 2).

Interspecific diet overlap was higher in Turkey, than in Manning Road Marsh, and overlap between juvenile bullfrogs and both classes of green frogs approached those of the intraspecific values between juvenile and adult bullfrogs in both marshes. However, as the size disparity between interspecific classes increases, overlap in diet drops markedly. The pattern is similar in the two marshes but in general overlap was lower in Manning Road Marsh. Thus adult bullfrogs and juvenile green frogs exhibit very little overlap at all. Consequently, as the size disparity between the bullfrog and green frog classes increases, the potential for competitive interactions decreases.

In contrast, the potential for asymmetric predatory interactions increases with increasing size disparity between species. This interaction is restricted almost exclusively to adult bullfrogs preying on juvenile green frogs. Of the frogs recovered from frog stomachs in Turkey Marsh, 90% (28 of 31) were at least 6 mm (SVL) smaller than the smallest juvenile bullfrog metamorph collected in the samples (the smallest bullfrog was 44 mm SVL). Thus, 90% of the frogs consumed could only have been green frogs. All frogs consumed may have been green frogs, since the largest individual consumed (51 mm SVL) was smaller than 96% of juvenile bullfrogs collected. Predation by bullfrogs on green frogs was not limited to major emergence times. Instead, it occurred regularly throughout the summer, a pattern similar to that reported in other studies (e.g., Korschgen, 1955).

The asymmetry in the postmetamorphic predator-prey interaction would tend to enhance the dominance of the bullfrog on the permanent pond end of the environmental gradient since it reinforces the asymmetry in larval interactions. That is, in ponds where larval bullfrog survival is favored by the presence of fish (Werner and McPeek, 1994, see also Corse and Metter, 1980; Hambright et al., 1986), the bullfrog can achieve a very large abundance advantage over the green frog in the subsequent terrestrial phase. Under these circumstances the few green frogs that metamorphose from these habitats will be vulnerable to a large population of predatory bullfrogs, and the resulting predation mortality should reinforce the advantage realized by the bullfrog in these permanent pond habitats. Indeed current evidence suggests that green frogs do not do as well when bullfrogs are in the same habitat (M. Stewart pers. comm., Collins and Wilbur, 1979). This potential of the bullfrog is also of concern in terms of its effect on native fauna in areas where it has been introduced (e.g., Hayes and Jennings, 1986). We clearly need experimental work on the impact of the interactions in the terrestrial stages of these species to predict the consequences of introductions of such species and the factors responsible for their distributions and success in native habitats.

Potential interactions between bullfrogs and green frogs are similar to those of many aquatic organisms where the interactions over ontogeny can switch from predatory to competitive or vice versa. From the bullfrogs’ perspective, the green frog is first a competitor when in the larval stage, and again when the postmetamorphic bullfrog is small, and then becomes simultaneously competitor (adult green frogs) and prey (juvenile green frogs) when the bullfrog is large. From the green frogs’ perspective, the bullfrog is a competitor in the larval stage, simultaneously a competitor and predator when the postmetamorphic green frog is small and a competitor when the green frog is large. Thus the ontogenetic pattern of potential interactions between the species is complex, and elucidating consequences for population and community dynamics will require detailed experimental work.

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