Diet of the Gray Treefrog (*Hyla versicolor*) in Relation to Foraging Site Location

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Abstract.—Despite growing concern over habitat destruction, little is known regarding the activities of pond-breeding amphibians in the terrestrial environment. Yet, because most pond-breeding amphibian species spend the majority of their time in terrestrial habitats, it is important to understand what role terrestrial habitat plays in their life history. We examined the stomach contents of the Gray Treefrog (*Hyla versicolor*) in central Missouri using a stomach-flushing technique. Treefrogs were stomach-flushed; stomach contents were dried and weighed; and prey items were counted and identified for frogs caught in both artificial arboreal refugia and at breeding ponds. The majority of prey consisted of ants (41.2%) and beetles (29.6%). Both males and females caught in artificial refugia contained greater stomach content mass than those caught at breeding ponds. There was a positive correlation between mass of stomach contents and distance from breeding ponds, with the average number of beetles per stomach increasing with distance from ponds. There was also greater stomach content mass in frogs found in artificial refugia on white oaks than red oaks or sugar maples, but there was no relationship between tree diameter and stomach content mass. These results demonstrate the importance of protecting terrestrial habitat to maintain foraging areas for treefrogs.

Habitat destruction poses a significant widespread threat to amphibian population persistence (Blaustein and Kiesecker, 2002; Semlitsch, 2003). Because many amphibians have a biphasic lifecycle, using both aquatic and terrestrial habitats (Wilbur, 1980), it is crucial to gain a better understanding of life history processes in both habitats to predict the effects of environmental changes on amphibian populations. Many studies investigating amphibian populations have focused on activities occurring at breeding sites (e.g., Berven, 1990; Beebee et al., 1996; Semlitsch et al., 1996) because large congregations of adults or emerging juveniles are relatively easy to sample. However, less is known about the activities and movements of amphibians in the terrestrial habitat adjacent to breeding sites (Marsh and Trenham, 2001; Lemckert, 2004) despite the realization that many amphibians spend the majority of their lives in upland terrestrial habitats (Semlitsch, 2000).

Although habitat loss is a primary threat to amphibian populations, indirect effects associated with habitat loss (e.g., changes in microclimate, alteration of trophic interactions) also likely affect the persistence of amphibians in disturbed sites. Trophic connections among taxa are an important component of the life history strategies of individuals and the regulation of populations (Wilbur, 1997). Therefore, an improved understanding of the roles amphibians play in food webs enhances our ability to maintain and restore natural habitats in the face of increasing anthropogenic changes. Arboreal anurans make intriguing subjects in the investigation of amphibian diets given their unique (among temperate amphibians) ability to exploit elevated foraging locations.

The Gray Treefrog, *Hyla versicolor*, is found in the eastern half of the United States (Conant and Collins, 1998) and has been hypothesized as an apex predator of natural tree-cavity food webs (Park et al., 1950). Previous studies have described the diets of arboreal anurans (e.g., Kilby, 1945; Freed, 1982), but the terrestrial versus aquatic activities of treefrogs have received limited attention (Lemckert, 2004). Our study provides an overview of the Gray Treefrog diet in terms of composition and prey abundance. Specifically, we compare the diet of males and females captured at breeding ponds with the diet of males and females captured in terrestrial habitat adjacent to breeding ponds. We expect that treefrogs captured in the terrestrial environment will have more stomach contents than treefrogs captured at breeding ponds. We also examine male and female treefrog diets with respect to distance from breeding ponds. Finally, we investigate the relationship between tree species and diameter and the diet of Gray Treefrogs.

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MATERIALS AND METHODS

Study Species.—*Hyla versicolor* is a nocturnal, moderately sized frog (32–51 mm SVL; Conant and Collins, 1998) that is abundant in central Missouri. Although *Hyla chrysoscelis*, the morphologically identical, diploid Gray Treefrog species, also occurs in Missouri, it does not occur in or around the study site (H. C. Gerhardt, pers. comm.). Gray Treefrogs breed from mid-April to mid-July, and males are found calling from low branches or bushes surrounding fishless, ephemeral ponds (Johnson, 2000). Male Gray Treefrogs leave breeding choruses on occasion to forage in the terrestrial habitat and replenish their energetic reserves, similar to other treefrog species (Gerhardt et al., 1987 [*Hyla cinerea*]; Ritke and Semlitsch, 1991 [*H. chrysoscelis*]; Murphy, 1994a,b [*Hyla gratiosa*]). Female Gray Treefrogs return to ponds once or twice per breeding season to deposit eggs (Ritke et al., 1990 [*H. chrysoscelis*]), spending most of their time in the terrestrial environment. During much of the year, including the breeding season, tree cavities are used as diurnal retreat sites (J. R. Johnson, unpubl. data). Tree cavities may also be used as sources of prey during nocturnal foraging bouts (Park et al., 1950).

Study Design.—This study was conducted in forest habitat surrounding three breeding ponds within the Baskett Wildlife Research Area in Boone County, Missouri, from 13 June until 15 July 2004. Terrestrial habitat adjacent to breeding ponds consisted of an oak/hickory canopy (*Quercus* spp./*Carya* spp.) with a maple/cedar understory (*Acer* spp./*Juniperus* spp.). We captured treefrogs by hand during nightly visits to breeding choruses and diurnally in artificial arboreal refugia made of black acrylonitrile butadiene styrene (ABS) conduit (see Johnson, 2005). These refugia (*N* = 98) were placed 3 m high in deciduous trees in transects (*N* = 7) extending up to 200 m from ponds into the terrestrial habitat. Gray Treefrogs use artificial refugia as they would use natural tree cavities. We checked refugia during daylight hours (between 1400 and 1800 h) when frogs were inactive. Refugia were designed to mimic the dark and humid conditions in natural tree cavities but not the arthropod abundance. Although two differing capture methods were used, we do not believe our results are biased for two reasons. First, refugia did not seem to provide an artificially inflated source of prey. Few prey were encountered in the artificial refugia during monitoring, and of the invertebrates that were present, most were spiders that were not found in high frequency within frog stomachs. Second, frogs were not found in the

artificial refugia at night, indicating that individuals using artificial refugia during the day would not be predicted to achieve greater foraging success during the evening. Furthermore, it would not be out of the question to predict greater foraging success at wetland-forest boundaries resulting from the combined presence of semiaquatic and terrestrial arthropod adults and emerging nymphs, which is in contrast to our results.

For each frog captured, we measured snout–vent length (SVL; to nearest 0.5 mm) using a plastic ruler, body mass (BM; to nearest 0.1 g) using a hand-held Pesola spring scale, and recorded sex using throat morphology. Each individual was given a unique mark via toe excision, and recaptures were recorded. Immediately following capture, each individual's stomach was flushed (as described below in Stomach-Flushing Techniques). Treefrogs were released at the capture site following stomach-flushing. Stomach contents were dried on filter paper and weighed to the nearest 0.001 g. Prey items were counted and identified to the lowest taxon possible.

We present comparisons using stomach content masses because this is a common dietary measurement (as reviewed in Hyslop, 1980). However, we also performed all comparisons using number of prey items instead of stomach content masses, and in all cases, we obtained highly similar results and reached redundant conclusions. Using two-tailed *t*-tests, we compared the average mass of total stomach contents from artificial refugia-captured treefrogs versus pond-captured treefrogs, as well as the average number of beetles or ants at both capture locations. Using linear regression, we analyzed the relationship between (1) distance from breeding ponds and stomach content mass, (2) tree diameter and stomach content mass, and (3) distance from breeding ponds and average occurrence per stomach content sample of only the two most common prey types (ants [Order: Hymenoptera] and beetles [Order: Coleoptera]), due to low sample sizes. We used ANOVA to determine the relationship between tree species and mass of extracted stomach contents from individuals captured in artificial refugia. Because of low sample sizes, only the three most common tree species (red oak [*Q. rubra*], white oak [*Q. alba*], and sugar maple [*A. saccharum*]) were included in these analyses. All stomach content mass data were natural log-transformed before analysis to meet the assumption of normality.

Stomach-Flushing Techniques.—Studies of amphibian diet vary in terms of the techniques used. Frogs may be euthanatized and stomachs extracted (e.g., Lamb, 1984; Donnelly, 1991;

Marshall and Camp, 1995), anesthetized and contents removed with forceps (Hirai and Matsui, 1999, 2000, 2001), or flushed with forcible injection of water through an inserted catheter (e.g., Legler and Sullivan, 1979; LeClerc and Courtois, 1993). We modified the techniques described by Patto (1998) and Sole et al. (2005) to apply the stomach-flushing procedure to the Gray Treefrog. We found no need for anesthesia because the legs could be immobilized using one hand. Instead of a spatula, the researcher's thumb was pressed lightly between the eyes to provide resistance while a catheter tube (< 1 mm inside diameter) was used to push up on the rostrum to force the mouth to open slightly for insertion of the catheter. A small amount of water squeezed from an attached 60 cc syringe was used as lubricant as the catheter was slid into the stomach. Once the tube was inserted and drawn back slightly to avoid rupture of the stomach, we found it necessary to orient the frog with its head downward. Patto (1998) and Sole et al. (2005) used 20 mL of water for small anurans; however, we found it necessary to use 60 mL to obtain all stomach contents.

The stomach-flushing procedure was repeated until no further stomach contents were produced, followed by one additional flush to ensure all contents were removed. Flushing usually produced contents in a large bolus along with small fragments of prey, which emptied into a small dish. We removed extracted stomach contents from the water using forceps, preserved contents in 2.0 mL vials of 95% ethanol, and returned them to the laboratory for analysis. We are confident that the stomach-flushing technique successfully removed all contents because continued bouts of flushing subsequent to bolus removal did not produce additional items. In addition, we conducted a preliminary study in which we fed five treefrogs a known number of crickets in the laboratory and used the stomach-flushing technique to produce all stomach contents successfully. Stomach-flushing was assumed to minimally impact behavior because, although we report only the first flushing of each individual, we flushed and obtained stomach contents from some individuals multiple times.

Results

We recorded a total of 526 captures of 308 individuals from 13 June until 15 July 2004, of which we stomach-flushed 107 individuals. From these individuals, 76 diet samples were obtained in which 204 total individual prey items were extracted (mean = 2.68 per frog, SE = 0.31, range = 0–13). Of the 31 individuals lacking stomach contents, 26 were males found at breeding ponds. Only 8% of males and no females caught in artificial refugia lacked stomach contents, compared to 38% and 29% at breeding ponds, respectively. The stomachs of 22 individuals contained plant matter, and six of these stomachs contained only plant material. In three instances, stomach contents were digested beyond our ability to identify them. The remaining 67 diet samples contained two subphyla, four classes, 11 orders, and 16 families (Table 1). Members of the family Formicidae were further classified into two subfamilies, three genera, and two species (Table 2). Of the identified orders, hymenopterans were the most numerous, comprising 41.2% of the total number of items, followed by coleopterans with 29.6% of the total; however, they occurred in 48 and 49 stomachs, respectively, of 76 stomachs from which contents were extracted (Table 1). Formicidae was the only family found within the order Hymenoptera.

We performed further analysis on the two main prey types (beetles and ants) with respect to sampling location (artificial refugia or ponds) and distance from breeding ponds. There was no difference in the mean number of ants extracted from frogs in artificial refugia or at ponds ($t_{35} = 1.597$, $P = 0.119$), but the mean number of beetles per stomach was greater for frogs captured in artificial refugia than those captured at ponds ($t_{37} = 2.177$, $P = 0.036$). Furthermore, linear regression of the number of beetles per stomach content sample extracted from frogs in artificial refugia showed a positive relationship with distance from breeding ponds ($N = 22$, $r^2 = 0.237$, $P = 0.010$).

Stomach content mass data indicated that males and females consumed similar amounts of prey ($t_{43} = 1.344$, $P = 0.186$). Further, an individual's length-specific mass (mm/mg) did not appear to influence the mass of prey ingested ($N = 75$, $r^2 = 0.024$, $P = 0.180$). Individuals captured in artificial refugia contained greater masses of stomach contents than individuals captured at ponds for both males ($t_{31} = 2.040$, $P = 0.001$; Fig. 1) and females ($t_{16} = 2.120$, $P = 0.004$; Fig. 1). There was a positive relationship between distance of artificial refugia from breeding ponds and stomach content mass of both males ($N = 14$, $r^2 = 0.423$, $P = 0.009$; Fig. 2) and females ($N = 11$, $r^2 = 0.476$, $P = 0.013$; Fig. 2). ANOVA revealed that there was a significant relationship between tree species and stomach content mass when DBH was a covariate ($F_{2,16} = 3.73$, $P = 0.047$; Fig. 3), and regression indicated that tree diameter was

TABLE 1.   Classification (Subphylum, Class, Order, Family) of prey items from stomach contents. 'Number of stomachs' indicates the number of frog stomachs containing prey of each type out of a possible 76. The total number of stomachs does not add up to the total number of frogs sampled because stomachs with multiple prey taxa were counted more than once. 'Mean per stomach' is the total number of items belonging to each taxon divided by the number of individuals from which stomach contents were extracted ($N = 76$).

	Number of items	Percentage of total	Number of stomachs	Mean per stomach
Mandibulata				
Insecta				
Hymenoptera				
Formicidae	84	41.2	48	1.11
Diptera				
Unidentified	1	0.5	1	0.01
Larvae	1	0.5	1	0.01
Lepidoptera				
Noctuidae	5	2.5	5	0.07
Larvae	8	3.9	7	0.11
Coleoptera				
Scarabaeidae	13	6.4	7	0.17
Elateridae	13	6.4	11	0.17
Lycidae	1	0.5	1	0.01
Buprestidae	1	0.5	1	0.01
Bruchidae	1	0.5	1	0.01
Cleridae	2	1.0	2	0.03
Coccinellidae	1	0.5	1	0.01
Curculionidae	5	2.5	4	0.07
Carabidae	3	1.5	3	0.04
Larvae	2	1.0	2	0.03
Unidentified	18	8.8	16	0.24
Hemiptera				
Pentatomidae	3	1.5	3	0.04
Unidentified	1	0.5	1	0.01
Orthoptera				
Gryllidae	2	1.0	2	0.03
Acrididae	1	0.5	1	0.01
Dictyoptera				
Blatellidae	11	5.4	9	0.14
Odonata				
Coenagrionidae	1	0.5	1	0.01
Crustacea				
Isopoda	1	0.5	1	0.01
Diplopoda	1	0.5	1	0.01
Chelicerata				
Arachnida				
Araneida	5	2.5	4	0.07
Phalangida	8	3.9	8	0.11
Unidentified	11	5.4	9	0.14
Total	204	100	151	2.68

not highly correlated with stomach content mass ($N = 26$, $r^2 = 0.087$, $P = 0.770$). Frogs captured in white oak trees contained greater stomach content mass than those captured in red oaks (least-squares mean [LSM], $P = 0.045$) or sugar maples (LSM, $P = 0.019$), but samples extracted from frogs captured in red oaks were not different from samples from frogs in sugar maples (LSM, $P = 0.606$).

DISCUSSION

Our study revealed that *H. versicolor* consumes a wide variety of terrestrial prey, mostly arthropods. No prey species limited to aquatic habitats was extracted from a treefrog stomach suggesting that minimal foraging occurs in breeding ponds. The high abundance of adult arthropods and absence of recently metamorphosed nymphs provides further evidence of

TABLE 2. Further classification (Order, Family, Subfamily, Genus, Species) of hymenopterans. Percentages were calculated from the total count of all items (from Table 1), not from the total number of hymenopterans observed.

	Number of items	Percentage of total	Number of stomachs	Mean per stomach
Hymenoptera				
Formicidae				
Unidentified	27	13.2	16	0.36
Formicinae				
Camponotus pennsylvanicus	14	6.9	11	0.18
americanus	7	3.4	6	0.09
Unidentified	16	7.8	8	0.21
Myrmicinae				
Crematogaster	5	2.5	1	0.07
Aphaenogaster	7	3.4	3	0.09
Unidentified	8	3.9	3	0.11
Total	84	41.2	48	1.11

the importance of terrestrial habitat adjacent to wetlands and provides evidence that foraging is not appreciable at the breeding ponds. However, we did observe a coenagrionid damselfly in one treefrog stomach, similar to a report by Horn and Ulyshen (2004) for *H. cinerea*, suggesting that opportunistic foraging may occasionally occur in close proximity to breeding ponds. We cannot fully discount the possibility that foraging occurred at breeding ponds during the early morning hours (i.e., 0000–0600 h) after sampling had occurred (2030–0000 h). Stomach contents would have been completely digested by the time we sampled individuals during that evening's breeding chorus. However, we find the scenario of early morning foraging unlikely based on a limited dataset comprised of individuals captured at the breeding ponds during daytime artificial refugia sampling. Three individuals were captured in artificial refugia located 1 m from the pond edge and produced an average of 1.7 ($\pm$ 0.7 SE) prey

items. Albeit from a small sample size, this average is more typical of the pond-captured individuals (mean = 1.9, $\pm$ 0.3 SE) than the artificial refugia-captured individuals (mean = 4.1, $\pm$ 0.5 SE).

Frog stomachs contained an average of 1.11 ants and 0.79 beetles, and ants and beetles constituted, respectively, 41.2% and 29.6% of the total number of prey items extracted. These high proportions relative to other prey types demonstrate a greater preference for and/or greater availability of these prey items, although we conducted no studies of prey availability at our study site. Ants outnumbered beetles in frog stomachs, but because the beetles are much larger than the ants, the beetles represent a greater proportion of the invertebrate biomass ingested by treefrogs and may be the most important component of their diet. Similarly, Redmer et al. (1999) found that beetles comprised the largest proportion of the diet of *Hyla avivoca*, a closely related congener. However,
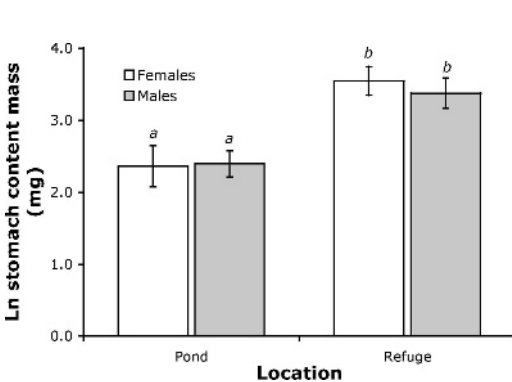

FIG. 1. Comparison of average stomach content mass (mg, ln-transformed) for males and females ($\pm$ SE) captured in artificial refugia and at breeding ponds. Letters denote *t*-test significance at $P < 0.05$.
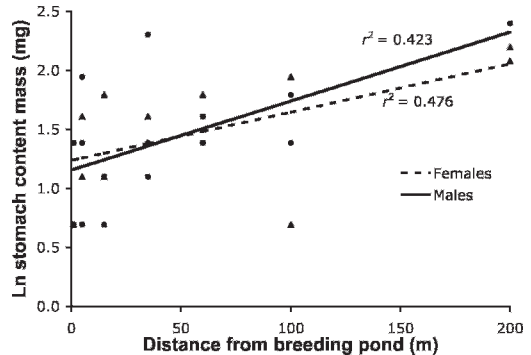

FIG. 2. Scatter plot displaying the relationship between distance of artificial refugia from breeding ponds and stomach content mass of males and females (mg, ln-transformed). Triangles denote female datapoints and circles denote male datapoints.
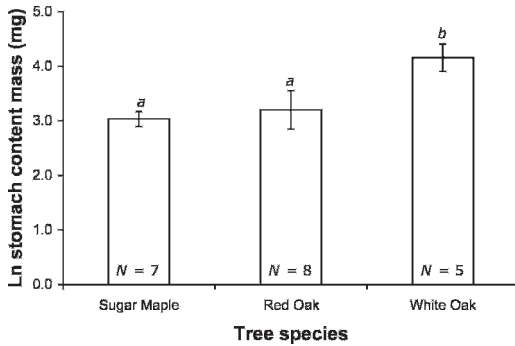
FIG. 3. Effect of tree species on average stomach content mass (mg, ln-transformed) for males and females combined (± SE). Sample sizes refer to the number of trees in each category, and letters denote LSM significance at $P < 0.05$.

because of their chitinous exoskeletons, ants and beetles take longer to digest and may be disproportionately represented in each stomach sample as compared to soft-bodied prey, such as larval lepidopterans, which were among the largest items ingested. Plant matter, including cedar (*Juniperus* spp.) needles and seeds, was found in 28.9% of stomachs. It is most likely that plant matter was ingested inadvertently when animal prey items were captured because most adult frogs are carnivorous (Duellman and Trueb, 1986). However, it is interesting to note that da Silva et al. (1989) report frugivory and seed dispersal in *Hyla truncata*, a Neotropical treefrog.

Individuals captured in artificial refugia contained greater stomach content mass than those captured at breeding ponds. This supports the hypothesis that treefrogs leave breeding choruses to forage at locations some distance away from breeding ponds and that foraging activity is minimal at ponds. Our data also show that mass of stomach contents was positively correlated with distance from breeding ponds, suggesting that higher quality foraging grounds may exist at greater distances from ponds. It is unknown, however, whether this relationship was the result of variation in prey abundance or reduction in conspecific competitor density. Although our linear regression equation shows a positive relationship between distance from breeding ponds and mass of stomach contents, many factors are likely involved in the foraging success of individuals, as is evident from the relatively loose fit of the model to the data (i.e., the low r^2-value). Additional sampling of individuals between the 100 m and 200 m sampling intervals would perhaps increase our understanding of the relationship between distance from breeding ponds and foraging success.

Beetles were ingested more often by frogs captured in artificial refugia than by frogs captured at breeding ponds, and the number of beetles per stomach increased with distance from ponds. However, there was no association of ant occurrence and capture location or distance from breeding ponds, suggesting a greater abundance of beetles in the terrestrial habitat. If beetles represent high quality prey, the ability to acquire more beetles as distance from breeding ponds increases may be an important factor in determining the migration distances of individuals and the terrestrial distributions of populations. Because no beetles were encountered in artificial refugia during regular monitoring, we assumed that the increase in beetle occurrence was not the result of capture method.

Stomach content mass was related to the species of trees in which artificial refugia captures were recorded. There was a significant trend for greater mass of stomach contents in frogs captured in white oaks than in red oaks or sugar maples. Attributes of white oaks (e.g., loose, furrowed bark) may provide better treefrog foraging sites, in terms of prey abundance or predator avoidance, than red oaks and maples. Although, without direct contemporary assessment of arthropod abundance at treefrog foraging locations spanning each tree species, it is difficult to make accurate generalizations regarding the effect of tree species on arthropod abundance, given seasonal and yearly variation in arthropod abundance observed in Missouri (Forkner et al., 2006).

Like most frogs, *H. versicolor* appears to be a generalist predator, with a diet superficially similar to that of other anurans (e.g., Kilby, 1945; Johnson and Bury, 1965; Oplinger, 1976; Hirai and Matsui, 1999). This work provides initial observations of variation in the composition and abundance of treefrog prey. Given the importance of trophic interactions to the ecology of species, future work should investigate seasonal differences in diet and prey availability and should experimentally test the effects of terrestrial habitat changes on the composition of amphibian diets. Acquisition of adequate prey resources likely affects factors (i.e., terrestrial population densities, individual fecundity) that directly influence population dynamics and deterministic extinction probabilities. Knowledge of amphibian diets during each life history stage is important for measuring the impact that anthropogenic habitat changes will have on the long-term persistence of amphibian populations.

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