Ontogenetic Behavioral Shifts in Habitat Utilization of Treefrogs (Hylidae) in North-central Florida

Michael C. Granatosky[1,2] and Kenneth L. Krysko[1]

[1]Florida Museum of Natural History, Division of Herpetology, P.O. Box 117800, University of Florida, Gainesville, Florida 32611, USA
[2]Present address: Department of Evolutionary Anthropology, P.O. Box 90383, Duke University, Durham, North Carolina 27708, USA
(michael.granatosky@duke.edu)

Photographs by Kenneth L. Krysko.

Natural history data through all stages of an animal's life cycle are necessary for making sound management decisions, which are especially critical in Florida, where developmental pressure often comes at the cost of species and their habitats. Despite being locally abundant, relatively little was known about ontogenetic behavioral shifts in habitat utilization for many hylid treefrogs. In this study, we used polyvinyl chloride (PVC) pipes to survey treefrogs in the localized, but habitat- and species-diverse University of Florida Natural Areas Teaching Lab (NATL) in north-central Florida. A variety of habitat variables were tested over multiple trapping seasons. We found that treefrog species were primarily limited by the presence of some water source or moisture, although some species were more tolerant of drier conditions than others. Ontogenetic shifts in habitat exploitation were detected only in limited instances, with juvenile Green Treefrogs (*Hyla cinerea*) demonstrating a narrower niche than adults, and juvenile Squirrel Treefrogs (*Hyla squirella*) being most commonly captured during winter and spring. The non-native Cuban Treefrog (*Osteopilus septentrionalis*) ranked third in species detection, and its distribution was highly limited by both season and habitat type. With much to be learned about amphibian biology and natural history, efforts should be made to continue local studies such as this to enable conscious management and conservation decisions.

Life history characteristics of species are important aspects to consider for both applied conservation and management practices. While many studies have addressed survivorship and reproductive potential, few have examined ontogeny. Ontogenetic shifts are not restricted to morphology, but apply to the entire life cycle of an organism. Appropriate studies of ontogenetic behavioral shifts are lacking in the literature, and these types of data for amphibians and reptiles are nearly absent. Treefrogs in the family Hylidae provide an excellent model to address such questions, because multiple species tend to be sympatric and syntopic, are abundant and congregate in large densities, and size classes are documented (Wright and Wright 1949).

Little information is currently known about life history characteristics of hylid treefrogs away from breeding ponds (Garton and Brandon 1975, Ritke and Babb 1991). Large numbers of treefrogs are not typically represented in herpetological surveys that employ drift-fence arrays, as tree-

Pine Woods Treefrogs (*Hyla femoralis*) occur in wetlands and upland pine at the NATL.

Green Treefrogs (*Hyla cinerea*) are the second most abundant species of treefrog at the NATL, where they frequently are found in all habitat types.

Squirrel Treefrogs (*Hyla squirella*) in a PVC-pipe refugium at the NATL.

Non-native Cuban Treefrogs (*Osteopilus septentrionalis*) are capable of consuming an array of both exotic and native invertebrates and vertebrates.

frogs easily escape by climbing out of pitfall and funnel traps (Gibbons and Bennett 1974, McComb and Noble 1981, Lohoefener and Wolfe 1984, Dodd 1991, Murphy 1993, Greenberg et al. 1994). Visual detection methodologies also are difficult, as treefrogs are generally small and often prefer densely covered habitats (Duellman and Trueb 1985). However, the use of polyvinyl chloride (PVC) pipes provides a simple and effective means to passively attract and thus sample treefrogs (Greenberg et al. 1994, Domingue O'Neill and Boughton 1996, Moulton et al. 1996, Boughton et al. 2000, Zacharow et al. 2002).

Currently, 14 native and one established non-native hylid species occur in Florida. All use generally similar habitats and are primarily restricted in distribution by the presence of a fresh water source, although some species are more tolerant of drier conditions and at least occasional exposure to brackish water (Wright and Wright 1949, Neill 1951). The use of PVC pipes can be effective for sampling multiple taxa, although in previous studies that have used them, not all species and size classes were represented equally (Domingue O'Neill and Boughton 1996, Moulton et al. 1996, Boughton et al. 2000).

Previous studies conducted in north-central Florida captured five arboreal hylids (Domingue O'Neill and Boughton 1996, Boughton et al. 2000). These included the Green Treefrog (*Hyla cinerea*), Pinewoods Treefrog (*Hyla femoralis*), Squirrel Treefrog (*H. squirella*), Spring Peeper (*Pseudacris crucifer*), and Cuban Treefrog (*Osteopilus septentrionalis*). The Spring Peeper has an expansive geographic distribution, ranging from southeastern Manitoba to eastern Texas. The Cuban Treefrog was first reported in Florida in the 1930s (Barbour 1931) and is now widespread throughout the peninsula (Meshaka et al. 2004). This treefrog thrives in habitats affected by anthropogenic disturbances, and has been found as far north as Canada (McGarrity and Johnson 2009). It is known to prey on many native invertebrates and vertebrates, such as lizards, frogs, snakes, and members of its own species (Meshaka 1996a, 2001; Krysko and Halvorsen 2010; Granatosky et al. 2011). While the diet of the Cuban Treefrog is relatively well documented compared to other non-native herpetofauna in Florida, additional information pertaining to the negative effects on the native faunal assemblage and how this species utilizes space could prove useful for management and control plans. The Green Treefrog, Pinewoods Treefrog, and Squirrel Treefrog have similar geographic ranges along the Atlantic and Gulf coastal regions of the southeastern United States (Wright and Wright 1949). These treefrog species share a similar distribution throughout Florida, and are more or less limited by the presence of fresh water and high humidity levels (Duellman and Trueb 1985). While proximity to fresh water plays an integral role in habitat utilization and selection, relatively little is known about taxon-specific or size-based habitat exploitation (Boughton et al. 2000).

Few studies have addressed the possibilities of ontogenetic habitat shifts in arboreal anurans. Dispersal has been defined as movement of an individual from one habitat to another, or away from the parental group (Jameson 1956, Semlitsch 2008). Dispersal not only affects the individual, but also influences inclusive fitness, genetic viability, and population dynamics. Many hypotheses seek to explain dispersal, and some assume that it is a mechanism to reduce potential inbreeding depression (Dunning et al. 1995, Hanski and Gilpin 1997, Hanski 1999) or incidence of parent/offspring competition (Dunning et al. 1995, Hanski and Gilpin 1997, Hanski 1999). While few studies have addressed the possibility of ontogenetic dispersal in treefrogs, some form of age-specific habitat distribution is likely (Jameson 1956).

Studies conducted over multiple trapping months have reported seasonal activity shifts in treefrog diversity and abundance, with both greatest in summer and late fall before decreasing during winter and early spring (Boughton et al. 2000; Johnson et al. 2007, 2008; Ackleh et al. 2010). This seasonal activity pattern is most commonly associated with cold winters, and populations of the exotic Cuban Treefrog tend to be more susceptible to colder conditions than their native counterparts (Meshaka 1996b). In this paper, we attempt to determine whether characteristics such as ontogeny, habitat type, pipe diameter, and pipe placement influence the sampling of hylid species at the Natural Areas Teaching Lab (NATL), University of Florida (UF), Gainesville, Alachua County, Florida. Additionally, we examined the diet of the Cuban Treefrog to determine the incidence of predation on native fauna.

Florida Water Snakes (*Nerodia fasciata pictiventris*) are frequently encountered in the wetlands of the NATL, where they feed largely on fishes and amphibians, facultatively consuming treefrogs of all life stages.

Gopher Tortoises (*Gopherus polyphemus*) occur in the upland pines and old-field succession of the NATL. They represent a keystone species, as their burrows are known to house more than 200 species of animals.

Materials and Methods

Study area.—This study was conducted at the NATL, located at 29.63434ºN, -82.36755ºW (WGS84 datum, 26 m elev.). The NATL is managed by the University of Florida and consists of 19.83 ha of four primary habitat types (hammock, upland-pine, wetland, and old-field succession). Due to the highly localized and diverse array of ecotypes, the NATL provides an ideal study area to address multiple questions related to ontogenetic habitat use in hylid treefrogs. Hammock habitat was defined as shaded, with thick stand of hardwoods and sparse pines; wetland habitat included some form of permanent water retention; upland-pine habitat was identified by well-drained soils and widely spaced longleaf pines with sparse understory vegetation; and old-field successional habitat was characterized by the presence of

Hammock habitat is characterized by thick stands of shade-tolerant hardwoods, few pines, and sparse understory vegetation. The area has well-drained soils that are relatively high in nutrients due to decaying organic leaf litter. Hammock ecosystems are common in north-central Florida.

Upland-pine habitat, often referred to as a sandhill ecosystem, occurs in upland areas with well-drained soils. A healthy upland habitat is dominated by widely spaced Longleaf Pines (*Pinus palustris*) with few understory shrubs and a dense ground cover of grasses and herbs.

Old-field habitat is a result of recently cleared land prepared for farming and then abandoned. Once abandoned, the area will slowly return to a wild state, but first must phase through transitional states with more or less predictable successional floral assemblages. A typical old-field succession in north-central Florida is dominated successively by annual weeds, blackberry and dog fennel, Loblolly Pine (*Pinus taeda*), and mixed hardwoods.

Wetlands are areas of lower elevation that include some form of permanent water retention. These areas also are characterized by the presence of ephemeral ponds that fill during rainy months. These ponds have no fish, facilitating amphibian reproduction and growth.

annual weeds and sparse hardwoods. Standard maintenance at the old-field site continually clears ground vegetation, and large dense hardwoods and pines are removed before they become established.

Sampling.—Ninety-six PVC pipes measuring 760 mm in length were divided into three size groups based on the internal diameter of the pipe (12.7, 19.1, and 25.4 mm). Pipes were evenly distributed across 16 randomly selected sites among the four primary habitat types. These pipes were further subdivided into two subgroups based on elevation; one group was placed in the ground and the other approximately 1.82 m above the ground.

Sampling efforts were divided into two trapping periods, opened continuously from 1 August–30 October 2010 and 6 January–15 March 2011, which allowed for examining potential effects of seasonal variation in treefrog abundance. One trap-day equaled one trap open for a 24-hour period. A 30-day acclimation period allowed treefrogs to locate and habitually utilize pipe refugia. Traps were checked *ad libitum* throughout the trapping session.

Upon capture, treefrogs were identified to species, and measured (± 0.03 mm) for snout-vent length (SVL) using Tresna Instrument IP 67 Waterproof Digital Calipers (www.Tresnainstrument.com). Native species were subsequently released unmarked at the capture site; however, all Cuban Treefrogs were removed as it is illegal to release non-native species without a permit from the Florida Fish and Wildlife Conservation Commission (Florida Statute § 379.231). Treefrogs observed perched on or next to pipe refugia were captured by hand and added to species totals. Captures were divided into size classes (i.e., juveniles or adults) based on previously published morphometric criteria for each species. Adults reported for each species include 37-mm SVL for the Green Treefrog, 25-mm SVL for the Pinewoods Treefrog, 23-mm SVL for the Squirrel Treefrog, 19-mm SVL for the Spring Peeper, and 28-mm SVL for the Cuban Treefrog (Wright and Wright 1949; Meshaka 2001). Removed Cuban Treefrogs were examined for stomach contents; invertebrates were identified to order and vertebrates to species. Representative Cuban Treefrogs were deposited as vouchers in the Florida Museum of Natural History.

Relative species composition and total captures were recorded. Pearson's chi-square tests were used to determine whether treefrog distribution was influenced by any habitat variables (habitat type, pipe elevation, pipe diameter, and seasonal activity), or by ontogenetic behavioral shifts between juveniles and adults of both Green Treefrogs and Squirrel Treefrogs. Statistical analyses were performed on quantpsy.org, an interactive calculation tool for chi-square tests of goodness of fit and independence (Preacher 2001) with $\alpha = 0.05$.

Results

In 15,360 trap-days, 549 total captures were made of five treefrog species: The Squirrel Treefrog, Green Treefrog, Cuban Treefrog, Pinewoods Treefrog, and Spring Peeper (Table 1). The latter two species were excluded from statistical analyses because of small sample sizes. High numbers of juvenile and adult Squirrel Treefrogs and Green Treefrogs allowed for analysis of ontogenetic shifts in habitat exploitation for these two species.

Hundreds of male Green Treefrogs (*Hyla cinerea*) congregate in wetlands, where the breeding choruses can be deafening.

Table 1. Species and age classes observed in the Natural Areas Teaching Lab (Gainesville, Florida), 08/2010–03/2011.

Species	Juveniles	Adults	Total
Hyla squirella	74	233	307
Hyla cinerea	76	113	189
Osteopilus septentrionalis	9	35	44
Hyla femoralis	0	8	8
Pseudacris crucifer	0	1	1
Total			549

Interspecific variation of species presence between the four habitat types suggested that captures were not randomly distributed (χ^2 = 43.920, df = 6, P < 0.001). The Squirrel Treefrog was the most cosmopolitan treefrog and was found in high densities in all habitat types, whereas the Green Treefrog was more restricted in its distribution. The Pinewoods Treefrog was captured in low densities throughout the site, and only one Spring Peeper was captured in the wetland habitat. The Cuban Treefrog was limited to certain habitats (Table 2). Both juvenile and adult Green Treefrogs (χ^2 = 4.563, df = 3, P = 0.206) and Squirrel Treefrogs (χ^2 = 5.663, df = 3, P = 0.129) were found randomly among the four habitat types.

Table 2. Total treefrogs observed throughout the study period in each of the representative habitats.

Species	Hammock	Wetland	Upland-pine	Old field
Hyla squirella	96	74	50	87
Hyla cinerea	59	73	22	35
Osteopilus septentrionalis	2	9	15	18
Hyla femoralis	3	4	0	1
Pseudacris crucifer	0	1	0	0

The Green Treefrog, Squirrel Treefrog, and the Cuban Treefrog utilized PVC pipe sizes differently from one another (χ^2 = 20.759, df = 4, P < 0.001). The Squirrel Treefrog was captured disproportionately more often (41.04%) in 12.7-mm diameter pipes than the other species, whereas the Green Treefrog was found most frequently (43.92%) in 25.4-mm diameter pipes. No particular pattern was observed for Cuban Treefrogs, as they appeared to show no preference for any of the three PVC pipe diameter sizes (12.7 mm = 38.64%, 19.1 mm = 36.64%, and 25.4 mm = 24.72%). Subsamples based on size-class revealed that juveniles and adults for both the Green Treefrog (χ^2 = 5.540, df = 2, P = 0.063) and Squirrel Treefrog (χ^2 = 2.333, df = 2, P = 0.311) did not utilize different PVC pipe diameters.

The Green Treefrog, Squirrel Treefrog, and Cuban Treefrog were captured more frequently (81.42%) in PVC pipes placed in the ground rather than on trees (18.58%), but did not utilize PVC pipes differently from each other (χ^2 = 0.026, df = 2, P = 0.987). We found no difference in pipe-height use between juvenile and adult Squirrel Treefrogs (χ^2 = 0.187, df = 1, P = 0.665). We did detect a significant difference in pipe-height use between adults and juveniles of Green Treefrogs (χ^2 = 5.986, df = 1, P = 0.014); juveniles were largely restricted to pipes placed in the ground (89.47%), whereas adults were less habitat-specific (ground = 75.22%, and tree 24.78%).

Treefrog abundance varied significantly between the two trapping periods (χ^2 = 23.799, df = 2, P < 0.001). Both Green Treefrogs and Squirrel Treefrogs were observed in relatively similar densities between the two trapping periods (Table 3). The Cuban Treefrog was more common in the first (84.09%) than in the second (15.91%) trapping period. Ontogenetic variation in seasonal treefrog abundance revealed differences in juvenile Squirrel Treefrog representation (χ^2 = 10.204, df = 1, P = 0.002). Juvenile captures were more common (67.11%) in the spring trapping period. No ontogenetic shift was observed in the Green Treefrog sample (χ^2 = 0.098, df = 1, P = 0.754). Graphic representation of the number and type of each treefrog captured also indicated seasonal trends in certain groups (Fig. 1). Cuban Treefrogs, juvenile Squirrel Treefrogs, and Pinewoods Treefrogs were captured more frequently in one trapping period than the other. All observations of Pinewoods Treefrogs were in the second trapping period, but due to small sample sizes, we could not dismiss the possibility of random captures.

Table 3. Treefrog captures observed between the two trapping sessions. The first trapping session (1 August–30 October 2010) was selected to represent environmental conditions of late summer and fall, while the second trapping session (6 January–15 March 2011) was selected to represent late winter through early spring. Seasonal variation in treefrog abundance was generally similar for *H. squirella* and *H. cinerea*. The seasonal abundance in *O. septentrionalis* varied significantly between the two trapping seasons. *Hyla femoralis* and *P. crucifer* were excluded from all analyses due to the low number of captures throughout the study period.

Species	Spring	Fall
Hyla squirella	145	162
Hyla cinerea	112	77
Osteopilus septentrionalis	37	7
Hyla femoralis	0	8
Pseudacris crucifer	1	0

We removed 44 Cuban Treefrogs ranging from 24.20–51.30 mm SVL. Eleven specimens (25.00%) contained at least one animal in their digestive tracts. Invertebrates made up a substantial portion (90.91%) of the contents identified and consisted of three orthopterans, two hymenopterans, two blattarians, and one each in the orders Areneae, Scorpiones, Hemiptera, and Lepidoptera. One anuran, a juvenile (21.30 mm SVL) Green Treefrog, was found in an adult Cuban Treefrog (49.50 mm SVL; UF 160926).

Discussion

This study demonstrates the effectiveness of PVC pipes as a means of capturing and sampling certain hylid treefrogs. We captured all of the five treefrog species known to occur at the NATL, although some capture biases were evident. Similar to previous studies (Boughton et al. 2000, Domingue O'Neill and Boughton 1996), Pinewoods Treefrogs and Spring Peepers were either more difficult to capture and/or less abundant than other species. Consequently, a different survey method should be used to effectively study these species. Despite certain capture biases, PVC pipes effectively captured Green Treefrogs, Squirrel Treefrogs, and Cuban Treefrogs. Whether this was a result of actual selection of PVC pipe refugia or relative abundance within each habitat type was not clear. The relatively low capture rates of Cuban Treefrogs might have been a result of low numbers at the beginning of the study (personal observation) and not an actual representation of selection for or against PVC pipe refugia; however, this species was found to be refuge-limited in southern Florida (Meshaka 2001).

Certain species captured throughout the study tended to be highly habitat specific. Due to similar ranges, both inter- and intraspecific competition was an expected consequence of resource limitations in a localized system. Despite being captured in large numbers in all habitat types, Squirrel Treefrogs were most commonly observed in old-field and hammock habitats.

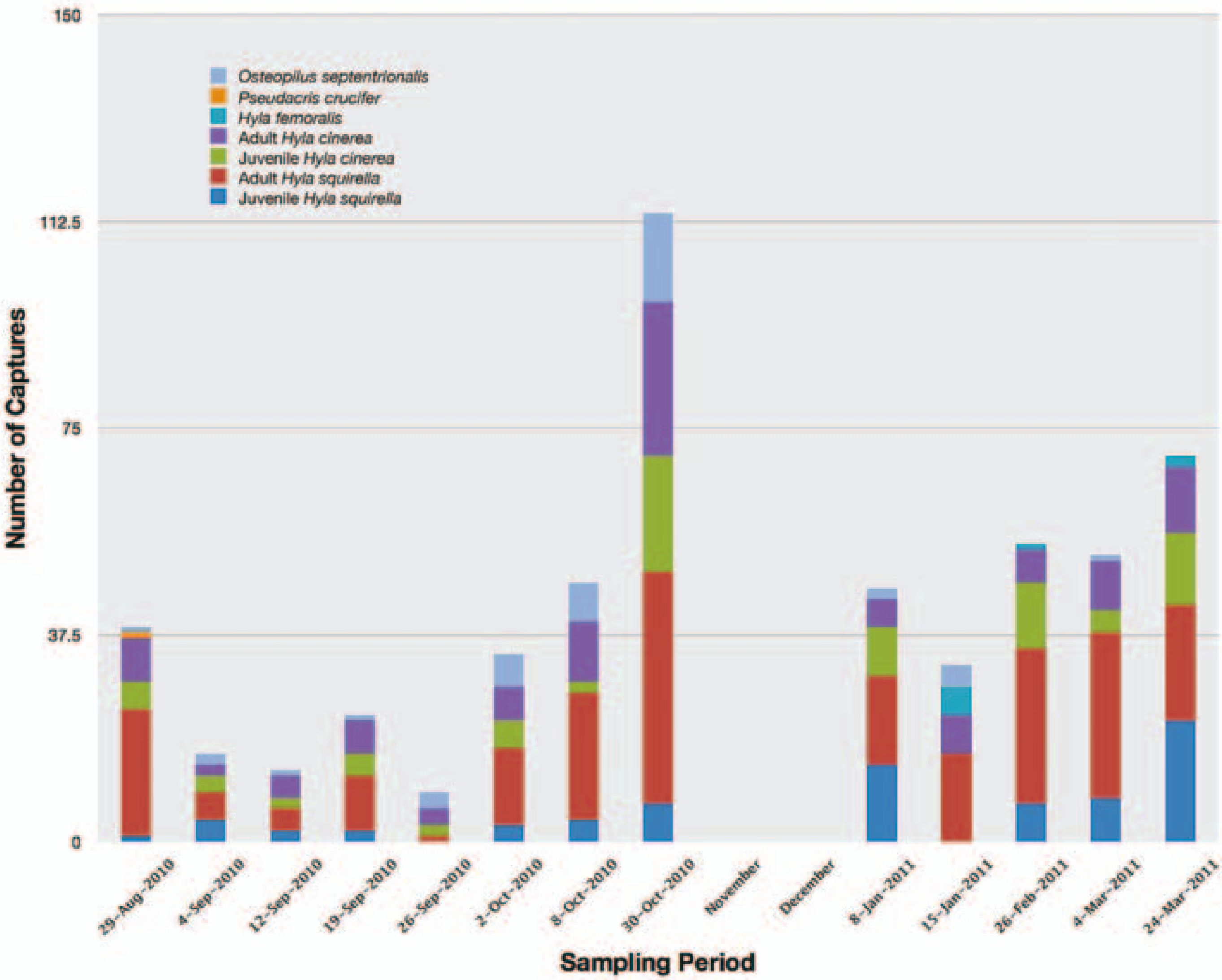

Fig. 1. Treefrog total and species representation observed throughout study. Differences in species captured appear to indicate that seasonality may be a driving force behind the presence or absence of particular types of treefrogs. Both exotic *Ostepilus septentrionalis* and juvenile *Hyla squirella* abundance tended to differ seasonally. Additional information also indicates that the presence of *H. femoralis* is seasonally driven, but due to low capture rates, we could not exclude the possibility of random observations.

The wide distribution of this species indicates that they are not limited by environmental conditions (i.e., moisture and vegetative composition), and distribution probably is limited only by the ability to find shelter or prey. Green Treefrogs were most abundant in hammock and wetland habitats, likely a result of moisture retention and heat. Although not tested, the thick canopy cover of the hammock habitat might have maintained sufficient levels of humidity (Goin 1958). The permanent source of water found in wetland habitat would have provided protection from desiccation. Non-native Cuban Treefrogs thrived in relatively disturbed environments (Meshaka 1996a), and the low disturbance factor of hammock habitat in the NATL might account for the low number of captures in that environment. The highest incidence of Cuban Treefrog captures was in old-field habitat, which is routinely managed in order to demonstrate early successional growth. Considering the rate at which natural ecosystems are becoming fragmented and/or developed, this exotic species likely will continue to thrive and spread into previously unoccupied regions. The versatility and resilience of these frogs also will render eradication plans difficult. Consequently, developing control plans, which could limit spread into new areas, might be more realistic.

Although some species appeared to utilize habitat types differently, Green Treefrogs, Squirrel Treefrogs, and Cuban Treefrogs demonstrated a strong tendency to use pipes placed directly in the ground rather than in a tree, and this seems to be a result of the amount of moisture that escapes from elevated pipes (see also Boughton et al. 2000). Constructing traps with some sort of water collection device (i.e., use of an end cap) might change capture rates in elevated pipes. Treefrog distribution was influenced by the internal diameter of refugia. Squirrel Treefrogs preferred smaller diameter pipes, whereas Green Treefrogs were more likely to use larger PVC refugia, suggesting that these species prefer the security of tight refugia close to the sizes of their bodies (Lee 1969, Wright and Wright 1949). Ontogeny appears to have little effect on how treefrogs utilize space. Both juvenile and adult Green Treefrogs and Squirrel Treefrogs did not use habitat types or pipe diameters in any predictable fashion, suggesting that suitable habitat was not a limiting resource. Limitations to population growth might instead be the result of some other factor such as prey availability, predation, or access to suitable breeding areas. The only observed instance in which ontogeny played some predictable role was in pipe elevations within the Green Treefrog data set. Our analysis indicated that juveniles were found disproportionately more often in ground pipes than adult conspecifics. Although ground pipes were preferred by all species and age-classes, adult Green Treefrogs appeared to be less selective, and a considerable number were captured in trees, suggesting that adult Green Treefrogs are more adept at exploiting potentially adverse conditions.

Dietary analysis of the Cuban Treefrog revealed that the majority of animal remains were invertebrates. Most notably, two different individuals (both 49.5 mm SVL) consumed native animals; one ate a Florida Striped Scorpion (*Centruroides hentzi*; 34.5 mm total length) (Granatosky et al. 2010), and one ate a Green Treefrog (juvenile 21.3 mm SVL). Meshaka (1996a, 2001) suggested that this exotic treefrog consumes an array of both exotic and native herpetofauna.

Previous studies (Meshaka 1996b, 2001; Boughton et al. 2000; Johnson et al. 2007; Johnson et al. 2008; Ackleh et al. 2010) demonstrated that treefrog abundance and distribution were influenced by seasonal climatic variation. We observed juvenile Squirrel Treefrogs in greater numbers in the spring sampling season, suggesting that as juveniles grow, they either use a different microhabitat in fall-winter or they venture away from these habitats. Cuban Treefrogs were most influenced by seasonal variation. This species is less cold-tolerant and cannot survive through sustained cold winters (Meshaka 1996a, 1996b). Managers should take advantage of cold weather conditions to remove and possibly eradicate localized Cuban Treefrog populations.

Due to recent declines in global amphibian populations, conservation action has been deemed important and essential for maintaining current population sizes as well as native biodiversity. The use of PVC pipe refugia has been demonstrated to be an effective means of capturing certain hylid treefrogs (Greenberg et al. 1994, Domingue O'Neill and Boughton 1996, Moulton et al. 1996, Boughton et al. 2000, Zacharow et al. 2002). Treefrog species tend to be limited in range by access to some source of fresh water or a means of retaining moist skin. Similar to other studies (Boughton et al. 2000), we found a great deal of variability in seasonal activity and in how treefrogs utilized space. Squirrel Treefrogs are extremely versatile and commonly found in large numbers across a wide range of habitat types, whereas Green Treefrogs appear to be limited by access to moist or humid conditions. Adult Green Treefrogs are more versatile in habitat exploitation than juveniles. At our study site, exotic Cuban Treefrogs were linked to disturbed areas. Because its superb colonizing abilities lower the likelihood of eradication in Florida, we believe that efforts would be better spent removing and controlling local populations. With much to learn about amphibian ecology and responses by amphibians to perturbations in their environment, studies such as this provide the sorts of life history data necessary for making informed resource management decisions.

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MIKE D. DUNN

Corallus annulatus from the Caño Palma Biological Station consuming what is likely a Brazilian Long-nosed Bat (*Rhynchonycteris naso*).