

Diet of the invasive Cuban Treefrog (*Osteopilus septentrionalis*) in pine rockland and mangrove habitats in South Florida

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ABSTRACT.—Native to Cuba, the Bahamas and the Cayman Islands, the Cuban Treefrog (CTF) is an invasive species in Florida, with the ability to inflict serious ecological damage to invaded habitats. By examining the diet of the CTF, a known predator of native frogs, better predictions may be made of the impacts on native species and ecosystems. From 2002 – 2003, CTF diet was investigated in south Florida at four sites, two each within pine rockland and mangrove habitat. Within each habitat, one site exhibited a low density of CTFs and the other a high density of CTFs. CTFs were captured in PVC pipes attached to trees and stomach contents were examined after euthanasia. Beetles were the most numerous and widely consumed prey item among sites; roaches, orthopterans, spiders, ants, and caterpillars were also major dietary components. There were significant differences in the proportion of taxa consumed by CTFs between low and high density populations within each habitat, with the low density site in every instance having the higher proportion. Across habitats, ants comprised a significantly higher proportion of the diet in mangroves, whereas beetles, orthopterans, and snails comprised a significantly higher proportion of the diet in pine rocklands. Approximately 3.5% of all stomachs examined contained anuran remains. Though not significant, CTFs from low density sites consumed a higher proportion of frogs than those at high density sites. Corroborating previous research, the data show the CTF to be a generalist feeder, consuming a wide variety of invertebrate prey, with anurans playing only a minor role in the overall diet.

KEYWORDS.—batrachophagy, Everglades, density effects, habitat effects

INTRODUCTION

The Cuban Treefrog (CTF), *Osteopilus septentrionalis*, is native to Cuba, the Bahamas, and the Cayman Islands (Schwartz and Henderson 1991), and is invasive in areas where it has been introduced in the Caribbean as well as Hawaii and Florida. The CTF has been established in mainland Florida since at least 1951 (Schwartz 1952), and its range continues to expand throughout the Florida peninsula (Johnson 2004; Krysko et al. 2005; Meshaka 1996). The success of the CTF as an introduced species in Florida is due to many factors, including a suitable subtropical climate (Meshaka 2001; Wyatt and Forsy 2004), the ability to thrive

in urban settings, short generation times, high fecundity, and the ability to produce eggs year round (Meshaka 2001).

Dietary plasticity and the ability to exploit a wide variety of prey items are also essential traits of a successful exotic species (Ehrlich 1989; Meshaka 2001). The CTF has been shown to consume a diverse prey assemblage in nature and in urban environments, consisting of primarily invertebrate prey, but also taking frogs and other small vertebrates (Maskell et al. 2003; Meshaka 1996, 2001; Meshaka and Ferster 1995; Owen 2005). Meshaka (2001) found that among all sites and size classes, dietary overlap between CTFs and native Green

and Squirrel Treefrogs was 55% and 41%, respectively. CTFs may be especially adept at exploiting available resources, including prey, possibly limiting native anuran abundance in CTF occupied areas. In laboratory experiments with larval anurans, CTFs were shown to have adverse effects on native anurans caused by strong interspecific competition (Knight et al. 2009; Smith 2005). The occurrence of CTFs has also been shown to sharply reduce the probability of occurrence of native treefrogs in south Florida (Meshaka 2001; Waddle et al. 2010). CTF diet is important to understand not only because native treefrogs are directly preyed upon by CTFs, but also because CTFs and native anurans share many of the same invertebrate prey.

The majority of diet studies have been conducted on CTFs from buildings or near human dwellings with nighttime light sources (Heflick 2001; Meshaka 1996, 2001; Owen 2005). There have been few diet studies in areas where CTFs are invasive in natural habitats, though Meshaka (2001) did examine CTF diet in semi-natural areas along trails, boardwalks, and overlooks in Everglades National Park. To better understand the effects of habitat and density on the diet of the CTF in natural areas, CTF stomach contents were compared in Everglades National Park at two mangrove and two pine rockland sites, with each habitat having one site with high CTF density and one with a relatively lower CTF density. Of particular interest was the prevalence of direct consumption of native frogs by the CTF across the two habitat types and densities.

MATERIALS AND METHODS

CTFs were sampled at four study sites within Everglades National Park, Florida, USA (Fig. 1). Sites were chosen *a priori* to represent areas with perceived low and high levels of CTF density in two habitats. Two of the sites, Long Pine Key and Research Road, were in pine rockland habitat, a fire-maintained pine savanna with shallow soil and weathered limestone outcrops and solution holes (Fig. 2-A). Overstory trees in pine rockland were exclusively South Florida

Slash Pine (*Pinus elliottii* var. *densa*), with an open understory maintained with frequent prescribed fires (Slocum et al. 2003). The other two sites, Flamingo and Harney River, were in mangrove habitat, with rainfall accounting for all the water available at Flamingo, whereas at Harney River, in addition to rainfall, occasional tidal flooding of near fresh water as well as sheet flow from the Everglades contributed to water availability at the site. Flamingo was located about 3 km from the visitor area and was dominated by a stand of mature Black Mangroves (*Avicennia germinans*). Harney River was located in a remote area of the river, and was located along a transition from Red Mangrove (*Rhizophora mangle*) to White Mangrove (*Laguncularia racemosa*; Fig. 2-B).

Artificial refugia were constructed of ca. 1 m lengths of polyvinyl chloride (PVC) pipes with a diameter of 5 cm to capture CTFs (Boughton et al. 2000). The pipes were hung vertically from nails left protruding from trees such that the top of the pipe was about 2 m above the ground (Fig. 2-A). Each pipe was open at the top, but the bottom was covered with a PVC end cap. A hole was drilled in the pipe about 5 cm up from the bottom to drain the pipe. This allowed each PVC pipe refuge to hold some rain water at the bottom when available.

There were 99 pipes set out at each site except for Long Pine Key. This site was originally two separate sites in close proximity, but due to low captures and habitat similarity the sites were combined so that the total was 198 pipes. Some trees at Flamingo, Harney River, and Research Road were outfitted with two pipes each, but all trees at Long Pine Key and most at the other sites had only one pipe per tree. All pipes were hung on mature Slash Pines at the two pine rockland sites and on mature Red, Black, or White Mangroves at the mangrove sites.

Sampling of the PVC pipe refugia was conducted as part of both an amphibian inventory of Everglades National Park as well as a more focused study on the effects of CTFs on populations of treefrogs native to Everglades National Park (Rice et al. 2004; Rice et al. 2011). Each PVC pipe

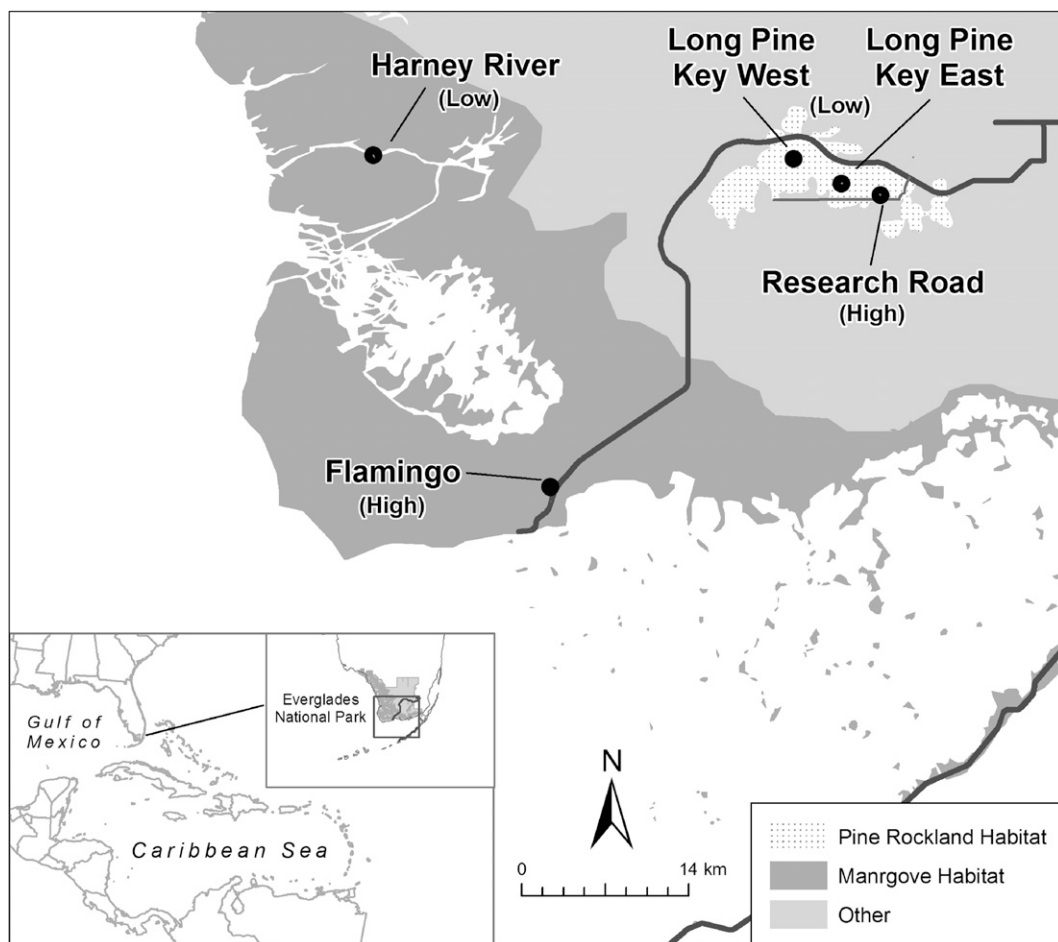


FIG. 1. Map of the study area within Everglades National Park. Due to low captures and similarity in habitat, Long Pine Key West and Long Pine Key East have been combined as simply Long Pine Key in the results. The inset shows the park shaded with the bounding box of the study area.

refuge was checked for treefrogs twice per month from 9 August 2002 to 1 August 2003. If present, CTFs were captured and placed in individual plastic bags marked with the site name and pipe number for processing. Native treefrogs were checked for marks, measured, and returned to the pipes. CTFs were euthanized via an overdose of Benzocaine (Chen and Combs 1999), measured for snout-to-urostyle length (SUL) to the nearest mm, and weighed to the nearest 0.5 g. The CTFs were then tagged with a unique number to relate them to the collection and morphometric data, fixed in 10% formalin, and stored in 70% ethanol solution.

A minimum density was determined at each site by using the number of individuals captured divided by the capture area. Using ArcGIS, the capture area at each of the four sites was determined by constructing a single minimum convex polygon with 5 m buffer around all trees sampled. Using this process, in pine rockland, Research Road had ca. 3 times the minimum CTF density of Long Pine Key. Likewise, in mangrove, Flamingo had ca. 5 times the minimum CTF density of Harney River.

The preserved stomach of each captured CTF was dissected out of the frog and examined for prey items. Each item found in the stomachs was identified to taxonomic order



FIG. 2. Photographs of (A) PVC pipe refugia on trees at the Research Road pine rockland site and (B) the Harney River mangrove site.

when possible. Unidentifiable prey or pieces of prey that could not be identified were listed separately. A Pearson's Chi-square analysis based on a 2×2 contingency table was used for comparison of counts of indi-

vidual stomachs that contained a given taxon versus those that did not, including empty stomachs, to determine if a given prey taxon was disproportionately eaten ($\alpha = 0.05$). Diet composition of stomachs at

low vs. high CTF density sites were compared within each habitat, and between the two habitats with both densities combined. All statistical analyses were performed in the R statistical package (R Development Core Team, 2009).

RESULTS

A total of 767 CTFs were captured from the four sites during the year-long removal period. Most of the CTFs (558; 73%) were collected from Flamingo, the high CTF density mangrove site. At Harney River, the low CTF density mangrove site, 113 CTFs (15% of the total sample) were collected. At Research Road and Long Pine Key, the high and low CTF density pine rockland sites, 68 (9%) and 28 (3%) CTFs were captured, respectively. Size of individuals varied by habitat and by CTF density (Fig. 3), where CTFs were larger at low density CTF sites relative to high density CTF sites (Two-way ANOVA, $F=102.21$, $p<0.001$) and at mangrove sites relative to pine rockland sites ($F=7.27$, $p=0.007$).

Of the 767 CTF stomachs that were dissected, 182 were devoid of contents (Table 1). Flamingo had the largest number of identified taxa (17) and Long Pine Key had the fewest (7). Research Road and Harney River

were intermediate with 8 and 12 identified taxa, respectively. Beetles, spiders, roaches, larval lepidopterans, gastropods, and anurans were found in at least one stomach at each site. Among all sites, beetles were found in more than twice as many stomachs as spiders, and nearly three times as many stomachs as larval lepidopterans.

Only at Harney River were beetles not found in the highest percentages of overall prey taxa, with roaches being equally present, and decapods (Mangrove Tree Crabs, *Aratus pisonii*) most numerous in examined stomachs. Twelve large CTFs (83 ± 11.5 mm body length, range 60-97; 43 ± 18.2 g body weight, range 12.5-77) consumed 16 Mangrove Tree Crabs. Ten of these individuals were checked for eggs and 6 were found to be gravid, with all but one of the 6 captured between May and July 2003. The other gravid crab-eating CTF was captured in October 2002. Because individuals were not sexed when dissected, the remaining 6 crab-eating CTFs may have been non-gravid females or large males. Of the 12 CTFs at Harney River that consumed decapods, only one also contained frog remains. The smallest CTF to have crab prey was 49 mm body length and 6 g body weight, and came from the lone occurrence outside of the Harney River at Flamingo.

The rate of batrachophagy among CTFs in this study was 3.52% of all stomachs examined. The two low CTF density sites had a higher, though not significantly different, proportion of batrachophagous individuals, approximately 4 and 1.5 times as many in pine rockland and mangrove habitats, respectively (Table 2). Batrachophagous CTFs appeared to be evenly distributed across adult size classes (Fig. 4). The Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis*) was found as a prey item in nine stomachs. The Green Treefrog (*Hyla cinerea*) was specifically identified in four stomachs, whereas frogs in other stomachs could only be identified as hyliid treefrogs. With the exception of a single 72 mm CTF that consumed three Eastern Narrow-mouthed Toads, all other batrachophagous CTFs contained one frog per stomach.

Comparing the prevalence of prey taxa among densities within a habitat, spiders

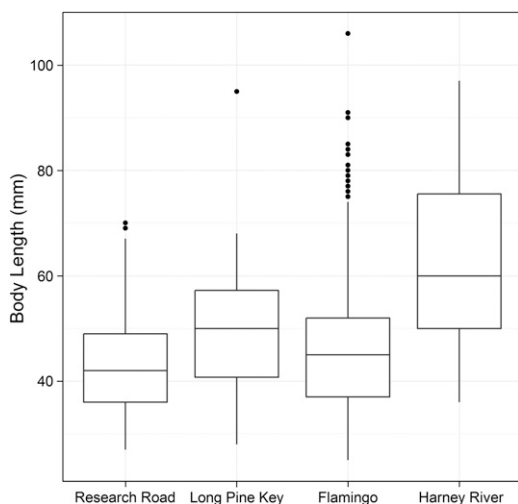


FIG. 3. Box plot of body lengths of Cuban Treefrogs collected from each of the four study sites. Points on the plot indicate probable outliers.

TABLE 1. Diet of the Cuban Treefrog (CTF) in pine rocklands with low CTF density (LPK – Long Pine Key) and high CTF density (RR – Research Road), and mangroves with low CTF density (Harney) and high CTF density (Flamingo). The total number of prey items found is followed by the number of stomachs containing given taxa in parentheses.

	LPK	RR	Harney	Flamingo	Total
# Frogs Dissected	28	113	68	558	767
# Frogs w/ Prey	22	100	55	408	585
# Empty	6	13	13	150	182
<hr/>					
Phylum Arthropoda					
Insecta					
Blattaria	1 (1)	3 (3)	9 (9)	16 (15)	29 (28)
Coleoptera	11 (5)	43 (29)	13 (9)	158 (92)	225 (135)
Diptera	0 (0)	0 (0)	7 (3)	5 (5)	12 (8)
Hemiptera	0 (0)	0 (0)	0 (0)	2 (1)	2 (1)
Hymenoptera	0 (0)	1 (1)	0 (0)	9 (8)	10 (9)
Formicidae	0 (0)	1 (1)	2 (1)	56 (39)	59 (41)
Lepidoptera	0 (0)	7 (4)	0 (0)	30 (23)	37 (27)
Orthoptera	3 (3)	15 (15)	9 (8)	26 (22)	53 (48)
Phasmatodea	0 (0)	0 (0)	2 (2)	1 (1)	3 (3)
Crustacea					
Decapoda	0 (0)	0 (0)	16 (12)	1 (1)	17 (13)
Isopoda	0 (0)	0 (0)	0 (0)	3 (3)	3 (3)
Arachnida					
Araneae	4 (4)	2 (2)	3 (3)	56 (48)	65 (57)
Chilopoda	0 (0)	0 (0)	0 (0)	4 (2)	4 (2)
Scorpiones	2 (2)	0 (0)	3 (3)	1 (1)	6 (6)
Phylum Mollusca					
Gastropoda	2 (2)	13 (11)	1 (1)	9 (8)	25 (22)
Phylum Chordata					
Anura	1 (1)	1 (1)	4 (4)	23 (21)	29 (27)
Squamata	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)
Mammalia	0 (0)	0 (0)	1 (1)	0 (0)	1 (1)
Skin	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)
Other					
Unidentified Invert.	0 (0)	27 (27)	1 (1)	25 (21)	52 (49)
Insect Matter	1	17	5	126	149
Unidentified Vert.	0 (0)	0 (0)	0 (0)	2 (2)	2 (2)
Unidentified	4 (4)	7 (7)	3 (3)	5 (5)	19

and scorpions were consumed significantly more at the low density pine rockland site relative to the high density pine rockland site (Table 2). Roaches, orthopterans, walkingsticks, decapods, and scorpions were consumed significantly more at the low density mangrove site than the high density mangrove site. By pooling the prey taxa in each habitat for both densities, ants had significantly higher prevalence in mangrove, whereas beetles, orthopterans, and snails had significantly higher prevalence in pine rockland, though these results may be associated with prey availability in the two habitats. Also, there were significantly

more empty stomachs in frogs collected from mangrove relative to pine rockland.

DISCUSSION

Beetles, spiders, orthopterans, ants, roaches, and caterpillars were the most commonly observed invertebrate prey items in the stomachs of CTFs in this study. Meshaka (2001) and Owen (2005) also found beetles, caterpillars, orthopterans, roaches, spiders, and ants to be primary components of the CTF diet. Despite these prey groups usually being most frequent in the diet of CTF, some site differences were observed with respect

TABLE 2. Chi-square analysis of stomach prey occurrence among low and high density CTF sites within pine rockland and mangrove habitats, and pooled across habitat types. The superscript letter above a bolded significant p value indicates the site with the higher stomach prey occurrence, or higher empty stomachs. Dashes indicate no observations of prey taxa at either density.

	Pine Rockland Low vs. High		Mangrove Low vs. High		Pine Rockland vs. Mangrove	
	Chi Square	p value	Chi Square	p value	Chi Square	p value
Blattaria	0.14	0.7082	15.54	<0.0001^L	0.10	0.7476
Coleoptera	0.38	0.5367	0.26	0.6074	4.52	<0.05^P
Diptera	-	-	3.48	0.0622	0.79	0.3731
Hemiptera	-	-	1.58	0.2081	0.67	0.4141
Hymenoptera	0.57	0.4483	0.18	0.6730	0.02	0.8936
Formicidae	0.57	0.4483	2.23	0.1351	6.26	<0.05^M
Lepidoptera	0.14	0.7082	1.86	0.1724	0.05	0.8146
Orthoptera	0.00	0.9624	6.50	<0.05^L	11.15	<0.001^P
Phasmatodea	-	-	4.77	<0.05^L	0.01	0.9387
Decapoda	-	-	82.56	<0.0001^L	1.86	0.1723
Isopoda	-	-	0.10	0.7461	0.01	0.9387
Araneae	5.83	<0.05^L	0.92	0.3381	2.00	0.1574
Chilopoda	-	-	0.41	0.5199	0.06	0.8089
Scorpiones	3.88	<0.05^L	11.09	<0.001^L	0.18	0.6744
Gastropoda	0.00	0.9525	0.27	0.6063	22.30	<0.0001^P
Anura	0.03	0.8543	0.26	0.6069	1.55	0.2127
Empty	1.14	0.2857	1.52	0.2183	9.35	<0.01^M

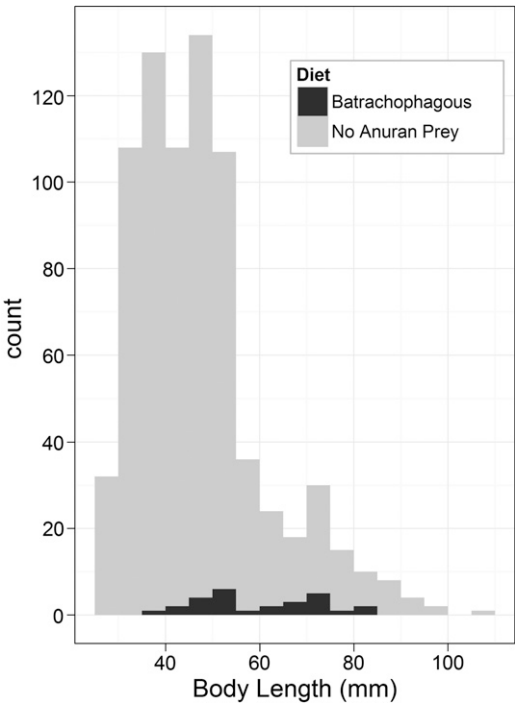


FIG. 4. Histogram of Cuban Treefrog body length showing the size distribution of batrachophagous frogs along with the distribution of frogs captured without anuran prey present.

to prey eaten, especially at Harney River, where Mangrove Tree Crabs, a previously unreported CTF prey item, constituted the greatest percentage of the CTF diet.

Besides one occurrence at Flamingo, Mangrove Tree Crabs were primarily found in the diet of CTFs from Harney River, the only site in the study that supported a robust population of crabs (J. H. Waddle, *pers. obs.*). The majority of crab-eating CTFs were some of the largest CTFs encountered in the study, and thus adult Mangrove Tree Crabs may not be as susceptible to predation by smaller CTFs. The novelty and dominance of Mangrove Tree Crabs as prey items in the diet of the CTF at this site underscores the opportunistic and generalist nature of the CTF as a predator.

Beever et al. (1979) found that the Mangrove Tree Crab plays a central role in the trophic structure of the mangrove community as a consumer, predator, and biomass exporter. The crabs feed largely on mangrove leaves, providing a significant input of biomass and possibly high quality nutrients to the marine environment in the form of frass (Beever et al. 1979). Many organisms also rely upon Mangrove Tree Crab eggs

and planktonic larva for food in the surrounding aquatic habitat (Beever et al. 1979). In addition, adult Mangrove Tree Crabs have few known natural predators (Beever et al. 1979; Odum et al. 1982), and therefore the invasion of CTFs into mangrove habitats may not only be detrimental to Mangrove Tree Crab populations but possibly to the stability of the entire mangrove ecosystem.

Despite reports of the CTF being a voracious frog-eater (Allen and Neill 1953), frogs in this study were found to comprise only a small percentage of the overall diet of the CTF, a result found in previous studies of CTF diet. Meshaka (1996) observed anuran prey in 3.03% ($n=99$) of CTF specimens from buildings in Everglades National Park, and Owen (2005) found anurans in less than 1% ($n=428$) of specimens obtained primarily from cisterns in the British Virgin Islands. In another study from the Everglades that included semi-natural areas as well as buildings, Meshaka (2001) reported anuran prey from 10.0% ($n=400$) of CTFs examined, with one semi-natural site having a batrachophagy rate of 19.4% ($n=62$). Heflick (2001) found Green Treefrogs in 18.9% ($n=53$) of CTFs captured from buildings with light sources in suburban Brevard County, FL. The batrachophagy rate of 3.52% ($n=767$) found in this study, within the range of previous studies, is of particular interest due to the large sample size from natural habitats.

Like Meshaka (2001), a similar wide range of body sizes of batrachophagous CTFs were found in this study (60.9 ± 12.9 mm body length; 40-83; $n=27$). Meshaka (2001) observed that large CTFs ate increasingly larger anurans. Both Heflick (2001) and Meshaka (2001) found 90% of their batrachophagous individuals to be female, which is the larger sex in this size dimorphic species. Larger CTFs may be able to consume a greater proportion of the size classes of native anurans. In this study, the majority of smaller batrachophagous individuals consumed the diminutive Eastern Narrow-mouthed Toad.

A higher, though not statistically significant, incidence of batrachophagy was observed at sites with lower density of CTFs in both pine rockland and mangrove habi-

tats. This trend is likely due to native frogs being more abundant at the low CTF density sites (Meshaka 2001; Rice et al. 2011), which may result in increased encounters of native frogs by CTFs. Wyatt and Forsys (2004) found that very large CTFs (mean snout-vent length = 67 mm) ate crickets first before Green Treefrogs or conspecifics in all cases when offered a choice in laboratory experiments. However, because CTFs hunt moving prey, these results may have been biased by abundant cricket movements in the terraria relative to treefrogs. Although a treefrog is a more nutritious meal than a cricket, a CTF predatory encounter with another treefrog can be energetically costly and not always successful (Meshaka 2001; Wyatt and Forsys 2004).

Examining CTF diet in the British Virgin Islands, Owen (2005) found a statistical difference in frequency of occurrence in 17 of 26 prey taxa when comparing stomach contents against intestinal contents, with all 17 prey taxa found more frequently in the intestine than the stomach. The overall composition of diet recovered from intestines and stomachs also differed significantly, with some taxa represented more often in stomachs, and some in intestines. Therefore, Owen (2005) recommended using both stomach and intestinal contents for a complete picture of diet. However, in this study, like Meshaka (1996, 2001), only stomach contents were used. Few identifiable prey taxa were located in the intestines and all were excluded from the analyses.

Monitoring treefrog populations using PVC pipes as a capture technique has been widely used due to its low cost and efficiency (Boughton et al. 2000). There is concern, however, that use of this technique may enhance predation by CTFs on native treefrogs. Wyatt and Forsys (2004) stated that because both native treefrogs and CTFs use the pipes, a density is created that may not be indicative of the natural environment. In this study, no direct evidence was found that treefrog monitoring using PVC pipes augments predation of native treefrogs by the CTF. Likewise, Hoffman (2007) found in laboratory studies that CTFs did not behaviorally exclude native treefrogs from pipe refugia, nor did pipes previously occupied

by CTFs deter native species from their use. Therefore, the rates of batrachophagy in this study are believed to be comparable to what occurs in nature at these sites.

It was believed initially that direct predation of native anurans would be the primary impact of invasive CTFs (Meshaka 2001). Based on this study of 767 CTFs it appears that batrachophagy is a minor component of the overall diet of the CTF in natural areas. However, native treefrogs are less likely to occur at sites occupied by CTFs in south Florida (Meshaka 2001; Waddle et al. 2010). Though predation rates of post-metamorphic individuals were found to be low, the cumulative effects of direct predation on all life stages as well as other processes, such as resource competition, are likely causes for the lower occurrence of native anurans observed in CTF occupied habitats relative to uninvaded areas.

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