INTRODUCTION

With continued urbanization, human-altered habitats must be increasingly considered as refugia for biodiversity. Effective management of natural remnants and artificial habitats in urban areas may serve as a partial solution to the loss of pristine ecosystems, while allowing for continued human use and economic profit (known as reconciliation ecology; see Rosenzweig 2003). As with traditional conservation methods, such efforts will benefit from regular monitoring of species abundance and population viability.

Mark-recapture is a particularly valuable tool for examining trends in vertebrate populations under certain conditions. Unfortunately, the need for high recapture rates is thought to reduce the utility of this method for rare or clandestine species such as snakes (Parker and Plummer 1987; Dorcas and Wilson 2009). As with traditional conservation methods, such efforts will benefit from regular monitoring of species abundance and population viability.

MATERIALS AND METHODS

Study site.—On the Eckerd College campus in St. Petersburg, Florida, USA, Omega (0.43 ha, excavated in 1996) and Zeta ponds (0.17 ha, excavated in 2004) were built to collect stormwater run-off (Fig. 1). A 10-m wide grass berm separated Omega from Zeta, but they remained connected by an underground pipe. Both ponds received an occasional influx of salt water during storms. Salinities varied from entirely freshwater (0.1 ppt) to slightly brackish (5-10 ppt). Water depth exceeded 2 m only near the center.
of both ponds. We documented a population of snakes since 2005, before intensive sampling began in 2006. Shorebirds, invertebrates, and several fish species had also been present for many years. For the majority of our study, the sloping pond margins were composed of mowed lawn, salt marsh grass (*Spartina* sp.), broom grass (*Andropodon* sp.), and cattails (*Typha* sp.). Trash, including bicycles and a computer monitor, accumulated in the emergent vegetation. Regularly mowed grass surrounded the study area, which was within 50 m of three college dormitories, a recreational field, and a parking lot. A beach facing Boca Ciega Bay paralleled the entire southern edge of Omega at a distance of about 20 m; there were patchy mangroves high up on the beach, but little protected shallow water usable by *Nerodia*. Several other ponds were present on the campus, with few outwardly apparent differences between them. However, one reason that led us to use Zeta and Omega was the absence of mangroves. During the summer 2007 sampling session (and unknown to us at the time), a maintenance subcontractor began applying the herbicide Aquamaster™ (glyphosate) in both ponds on a monthly basis to reduce invasive cattails (see Monsanto Company, Material Safety Data Sheets, Aquamaster[TM] Herbicide. 2004. Available from http://plants.ifas.ufl.edu/guide/aquamaster_msds.pdf [Accessed February 09 2010]).

**Sampling techniques.**—Using headlamps at night, we attempted to hand-capture all observed snakes while walking in a ~1–3-m wide strip of emergent vegetation near the shoreline. We made approximately one circuit of the perimeter of each pond, usually with three to five experienced students (the number of observers varied with student availability). Captured snakes were returned to the lab. We dorsally injected unmarked snakes > 40 cm snout-to-vent (SVL) with subcutaneous passive integrated transponder (PIT) tags. We judged snakes < 40 cm to have too little muscle mass for this tagging method, and, therefore, we were unable to integrate this size class into mark-recapture estimates. Snakes were typically released 24 hours after capture. Rarely, we held snakes for two or three days to complete collection of data, including size, weight, and a visual estimate of reproductive status in females (we determined sex by tail shape; females > 40 cm were assumed to be mature). Our measurements are presented as mean ± one standard deviation. We based each seasonal population estimate on three nights of sampling: spring 2006 (6, 18, and 26 April), spring 2007 (29 March, 2 April, and 25 April), summer 2007 (28 May, 7 June, and 30 July) and fall 2007 (12 August, 30 August, and 1 October). During the spring 2006 sample, we only captured *N. c. compressicauda* > 40 cm. We caught snakes of all sizes in subsequent samples.

**Data analysis.**—We generated seasonal population estimates of snakes > 40 cm (N>40) using Schumacher’s closed population model, with 95% confidence interval (CI; Schneider 2000). If CIs did not overlap, we assumed a change in N>40 to represent a significant change in population size between seasons. When generating estimates, we treated recaptures from previous sampling seasons as newly marked animals. We determined a seasonal biomass by multiplying the mean seasonal weight of snakes > 40 cm by the population estimate. We performed t-tests (α = 0.05) with SPSS 16 (SPSS Inc., Chicago, Illinois, USA) to determine changes in mean body mass between seasons.

**RESULTS**

We used data from 413 snakes captures between April 2006 and October 2007 in our calculations. Our population estimates showed considerable variation among seasons, and indicated significant population growth from spring 2006 to spring 2007 (Table 1). The first herbicide application occurred during the summer 2007 sample (exact
date unknown), while our population estimate remained stable. Several dense patches of cattails and other emergent vegetation died in late July, but remained upright. This dead vegetation collapsed into the pond during August. Our subsequent population estimate decreased significantly to 47 snakes (78/ha) in fall 2007. Within-season recapture rates, defined as the mean percentage of snakes > 40 cm we captured in the second and third seasonal sampling nights that bore PIT tags from the first night, ranged from 22% (summer 2007) to 45% (spring 2006). Overall recapture rates (the mean percentage of previously tagged snakes > 40 cm in all three samples) increased over the last three seasons from 47% to 68% and finally to 75% in fall 2007.

Marked snakes ranged from 40 cm to 85 cm SVL (mean 51 ± 10 cm). The mean weight of snakes > 40 cm was 163 ± 5 g. Biomass of this size class was initially 9.4 kg/ha in spring 2006, and peaked at 25.4 kg/ha in spring 2007. We observed three snakes in late April 2007 that may have been gravid; 12 of 32 unique females > 40 cm caught during the summer 2007 samples (May, June and July) appeared to be carrying young. We caught no obviously gravid snakes after July.

Unmarked snakes ranged from 19 cm to 39.5 cm SVL (mean 31 ± 5 cm). During spring, summer, and fall 2007, snakes < 40 cm increased from 37% to 43% to 53% of total nightly captures, with the balance being in the > 40 cm size class. Concurrently, mean body mass of snakes < 40 cm significantly decreased between spring 2007 (mean 0.036 kg) and summer 2007 (mean 0.029 kg; \( t = 2.19, df = 99, P = 0.031 \)). A further decrease in mean body mass between summer 2007 (mean 0.029 kg) and fall 2007 (mean 0.024 kg; \( t = 1.97, df = 106, P = 0.052 \)) approached significance. Snakes < 40 cm accounted for 11–14% of all captures by weight.

The maximum density we observed, 159 snakes (> 40 cm/ha), was also high. The median density from nine other natricine snake studies was 22/ha and ranged from 1–1289/ha (Parker and Plummer 1987). Parker and Plummer (1987) compiled 57 density estimates for 40 snake species, the highest reported being 4.58 kg/ha. Exceptions have occurred for aquatic snakes when habitat area and prey availability are affected by drought, producing estimates of 50 kg/ha for Acrochordus arafurae (Shine 1986) and 30.8 kg/ha of water hyacinths for Regina alleni (water hyacinths were used as a proxy for available habitat; see Godley 1980). Interestingly, Godley (1980) also sampled a modified aquatic habitat (dredged canals on either side of a road), though not in an urban context as was our study. Our biomass estimates are biased downwards due to the exclusion of snakes < 40 cm (this size class accounted for 11–14% of all captures by weight).

We documented extensive use of two urban stormwater retention ponds by Nerodia clarkii compressicauda. This water management project was completed only two years prior to our study, and represents an inadvertent example of reconciliation ecology (Rosenzweig 2003). Despite being seemingly inhospitable, the artificial wetland supported a snake biomass of 25.4 kg/ha, one of the highest ever found for a residential population of sedentary vertebrates (Bonnet et al. 2002). Iverson (1982) reviewed biomass data for 38 snakes species, the highest reported being 4.58 kg/ha. Exceptions have occurred for aquatic snakes when habitat area and prey availability are affected by drought, producing estimates of 50 kg/ha for Acrochordus arafurae (Shine 1986) and 30.8 kg/ha of water hyacinths for Regina alleni (water hyacinths were used as a proxy for available habitat; see Godley 1980). Interestingly, Godley (1980) also sampled a modified aquatic habitat (dredged canals on either side of a road), though not in an urban context as was our study. Our biomass estimates are biased downwards due to the exclusion of snakes < 40 cm (this size class accounted for 11–14% of all captures by weight).

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**DISCUSSION**

**TABLE 1.** Population size (95% confidence interval) and biomass estimates of Mangrove Salt Marsh Snakes (Nerodia clarkii compressicauda) > 40 cm snout-vent length at Omega and Zeta ponds on the Eckerd College campus in St. Petersburg, Florida, USA. An herbicide was used on the habitat during the 2007 summer sample. An asterisk indicates a significant change in population size from the previous season.

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<tbody>
<tr>
<td>Spring 2006</td>
<td>27</td>
<td>33 (26–40)</td>
<td>55</td>
<td>9.4</td>
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<tr>
<td>Spring 2007</td>
<td>67</td>
<td>95 (59–131)*</td>
<td>159</td>
<td>25.4</td>
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<tr>
<td>Summer 2007</td>
<td>52</td>
<td>94 (72–115)</td>
<td>157</td>
<td>25</td>
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<td>Fall 2007</td>
<td>33</td>
<td>47 (42–52)*</td>
<td>78</td>
<td>12.5</td>
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*We extrapolate population size and biomass of snakes < 40 cm using the proportional capture rate of this smaller size class;
Aquamaster™ (glyphosate) is considered to be slightly toxic to birds, and practically non-toxic to invertebrates and fish, but it was not tested on reptiles (see documentation in methods). As we learned of the herbicide months after it was applied, we could not quantify indirect effects of changes in prey availability or bioaccumulation and magnification. We believe emigration due to the proximate change in physical habitat structure was the most likely cause, as our estimates remained high when the initial chemical applications occurred and while the dead vegetation continued to provide cover during summer 2007. In a study of American Alligators (Alligator mississippiensis), the elimination of cattails and other emergent vegetation associated with a deliberate reduction of water depth in an artificial reservoir resulted in low levels of emigration and reduced recruitment (Brisbin et al. 2008). Emigration following drought has also been observed in Nerodia and Seminatrix, presumably due to natural fluctuations of water levels and prey availability (Seigel et al. 1995). We did not observe any large changes in water level; however, herbicide may have functioned in a manner analogous to natural disturbances at our urban study site. Seasonal demographic fluctuations could also have been a contributing factor (e.g., Winne et al. 2005), but as is often the case with urban field studies, experimental replication and control of anthropogenic habitat modification is difficult (Windmiller et al. 2008).

Our results could have been influenced by changes in snake detection probability and environmental variation. Due to intensive searches of a small habitat in an open area with good visibility, we do not believe that alterations of vegetation structure (natural or anthropogenic) greatly influenced visual surveys or snake capture rates. Following the use of herbicide, if an even more open habitat had resulted in higher detection rates (e.g., Brisbin et al. 2008), the actual population decline in fall 2007 would have been even greater than our estimates suggest. We believe that differences in detection probabilities between our study ponds and the other water bodies on campus could only be responsible for a small part of the difference in encounter rates of 50 snakes/hour in our 0.6 ha study area and encounter rates 1–2 snakes per year on the entire ~70 ha campus.

Violations of closed population assumptions (e.g. no mortality, migration, or recruitment) were minimized by several factors: (1) Each season’s marks were treated independently; (2) Data for each seasonal estimate were collected within a relatively short timeframe; (3) Capture histories and regular surveys suggest that our population was restricted to the area we sampled, the snakes used both ponds as a single habitat, and that no large source or sink populations existed nearby; and (4) Because unmarked snakes < 40 cm could not be incorporated into the population modeling equation, closed population violations within this size class (e.g. birth) should have had minimal influence on our results for larger snakes.

Snakes < 40 cm could have been directly incorporated into our model if we had injected PIT tags into the body cavity, rather than the dorsal musculature. However, this has lead to serious injuries in small snakes (Keck 1994). We also did not incorporate palpation, probing, and other tagging methods (e.g. scale clipping and branding) due to risk of injury. These were both personal and Institutional Animal Care and Use Committee decisions based on our unique circumstances. Our project was used to instruct a variety of undergraduates (with a variety of majors) in field sampling procedures, and involved people with less experience than graduate students and professionals. We knowingly sacrificed a degree of rigor due to safety concerns for our study animals.

Considering that these urban ponds were recently constructed for the purpose of collecting runoff from chemically treated recreational fields and a nearby parking lot, the mere presence of high trophic level predators larger than 1 m in total length was unexpected. However, instances of watersnakes achieving high densities in modified habitats have been previously documented (e.g. Godley 1980; Keck 1998; Lacki et al. 2004). While N. compressicauda appeared to be a temporary beneficiary of this artificial habitat, the possibility of biomagnification and snake emigration could potentially function as a vector of pollutants, thus reducing the ponds’ retention capability. Future investigations of source and sink metapopulation dynamics and habitat connectivity should attempt to determine how urban populations influence, and are influenced by, nearby communities (urban or otherwise). If novel habitat characteristics that affect population persistence and carrying capacity are successfully applied in urban wildlife management, habitats like stormwater retention ponds could become biologically productive while fulfilling their anthropocentric purpose.

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Herpetological Society’s assistance with data collection was invaluable, especially the contributions of Guy Keickehefer, Kenneth Chapin, Moses Michelsohn, and Kimberly E. Schmidt. Particular gratitude is due to the administration of Eckerd College in providing information on herbicide use. Dean of students, Lloyd W. Chapin, along with Luz Arcila, Ryan Arnold, and the Environmental Affairs Committee have been supportive throughout this study, and with the consideration of these individuals, a non-destructive ecological management plan including native plantings is being implemented.

**Literature Cited**


JEFFREY W. ACKLEY conducted this project while an undergraduate at Eckerd College, where he graduated with a B.S. in Biology and minors in East Asian Studies and Japanese. He served as a Teaching Assistant for ecology and herpetology classes, and was the vice president and co-founder of the EC Ale Connoisseurs. Jeff has participated in two NSF summer research programs: Experimental Field Biology at Sam Houston State University, Texas; and Natural History of a West Indian Herpetofauna at Avila University. He recently received a NSF Integrative Graduate Education Research Traineeship in Urban Ecology at Arizona State University, where he is beginning his doctoral studies of reptile and amphibian diversity within the Phoenix metropolitan area. (Photographed by Richie Moretti)

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