Frequent Consumption and Rapid Digestion of Prey by the Lake Erie Watersnake with Implications for an Invasive Prey Species

Peter C. Jones[1], Richard B. King[1], Kristin M. Stanford[1], Tyler D. Lawson[2], and Matt Thomas[3]

Studies of interactions between invasive and native species often focus on impacts on natives. We report potential impacts of a native predator, the Lake Erie Watersnake (*Nerodia sipdeon insularum*) on an invasive fish, the Round Goby (*Apollonia melanostomus*). Round Gobies have increased exponentially in the Great Lakes and now constitute >90% of prey consumed by Lake Erie Watersnakes. We investigated the effects this shift may have on round goby populations by estimating total prey consumption by Lake Erie Watersnakes. Digestive rate trials and maximum voluntary prey consumption trials indicate that gastric digestion is rapid (digestion was 90% complete after just 16.4 hours at 30°C and 20.1 hours at 25°C) and voluntary prey consumption is high (from 30.0% of adult female body mass to 117% of neonate body mass in five days). Based on palpation of wild-caught snakes, prey were detected more frequently in adult females than adult males, but no such difference was observed in subadults. The proportion of snakes containing prey varied over time with season-long averages of 11.6% for adult females, 6.9% for adult males, and 22.4% for subadults. Systematic surveys by boat indicate that nearly 90% of foraging occurs <150 m from shore. Projected annual consumption, based on gastric digestion rate, maximum voluntary prey consumption, feeding frequency of free-ranging snakes, and published energetic data and a population size of 12,000 adult watersnakes, ranges from 200,000–3,300,000 Round Gobies (4,455–56,178 kg) per year. Although impressive, this rate of prey consumption is unlikely to have more than local effects on Round Goby populations.

INVASIVE species are widely recognized for the impacts they have on native species, communities, and ecosystems (Mooney et al., 2005; Pimental et al., 2005), but detailed understanding of the interactions between invasive and native species is often lacking. One such interaction occurs when an invasive species displaces the prey of a native predator. Examples include Cane Toads and Australian snakes (Phillips and Shine, 2004), Manila Clams and Eurasian Oystercatcher (Caldow et al., 2007), Golden Eagles and feral pigs (Roemer et al., 2002), and Round Gobies and Lake Erie Watersnakes (King et al., 2006a). Invasive toxic Cane Toads have generally had a negative impact on Australian snakes (Phillips et al., 2003). However, some Australian snake species exhibit evolved responses in body size, relative head size, physiology, and behavior in response to natural selection imposed by Cane Toads (Phillips and Shine, 2004, 2006). In contrast, invasive species sometimes appear to have beneficial effects on native predators. Invasive Manila Clams reduce the over-wintering mortality of Eurasian Oystercatchers (Caldow et al., 2007). Golden Eagles were able to colonize the Californian Channel Islands due to the availability of feral pigs, although the eagle caused a decline in endangered Island Foxes through increased predation (Roemer et al., 2002). Lake Erie Watersnakes (*Nerodia sipedon insularum*) have benefited from the invasion of Round Gobies via increased growth rate, body size, and fecudity (King et al., 2006a, 2008).

The Round Goby (Gobiidae: *Apollonia melanostomus*) is native to the Sea of Azov and in near-shore areas of the Black Sea, Caspian Sea, and Sea of Marmara (Charlebois et al., 1997). Round Gobies were introduced to the Great Lakes in the early 1990s through ballast water carried by trans-Atlantic ships (Jude, 1997). The Round Goby population expanded rapidly, and the fish were found throughout the Great Lakes soon after introduction (Marsden and Jude, unpubl.). Round Gobies feed on two other invaders from the Caspian Sea region, Quagga and Zebra mussels (Ray and Corkum, 1997). Round Gobies also feed on the eggs of several native fishes including Yellow Perch, Walleye, Smallmouth Bass, Shiners, and Roughbelly Darters, and they compete with Mottled Sculpins and Logperch for space and food (Janssen and Jude, 2001). By 2005, there were an estimated 9.9 billion Round Gobies in just the western basin of Lake Erie (Johnson et al., 2005).

The Round Goby reaches a total length of 215–290 mm at maturity and is easily distinguished from native North American fish by its fused pelvic fins, which form a suction disk (Miller, 1986). Round Gobies mate several times throughout the year and captive females lay five to six clutches of 200 to 9,771 eggs 18–20 days apart (Kovtun, 1977). Females deposit eggs in cavities where they are guarded by the spawning male until hatching (Miller, 1986). During nest guarding, the male's color changes from gray-green to black (Miller, 1986). Round Goby life history differs between native and invasive populations (MacInnis and Corkum, 2000a, 2000b) in that invasive Round Gobies reach sexual maturity earlier (one vs. two years of age) and at a smaller size (MacInnis and Corkum, 2000b). Although invasive females lay fewer eggs per clutch, they still have higher fecundity than native species (MacInnis and Corkum, 2000a).

The western basin of Lake Erie is also home to the Lake Erie Watersnake, *Nerodia sipedon insularum* (Conant and Clay, 1937), which is listed as threatened in the U.S. and endangered in Ontario, Canada and Ohio, USA (Fazio and Szymanksi, 1999). This non-venomous colubrid snake is found only in the island region of western Lake Erie, an area that includes 18 islands ranging from 0.5–4260 ha and 0.3–

[1] Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115; E-mail: (PCJ) pjones2@niu.edu; (RBK) rbking@niu.edu; and (KMS) theislandsnakelady@yahoo.com. Send reprint requests to PCJ.
[2] Master of Environmental Studies Program, College of Charleston, 66 George Street, Charleston, South Carolina 29424; E-mail: tylaw02@hotmail.com.
[3] F.T. Stone Laboratory, The Ohio State University, P.O. Box 119, Put-In-Bay, Ohio 43456; E-mail: thomas.347@osu.edu.

22.4 km from the mainland (King et al., 2006a). Prior to the Round Goby invasion, Lake Erie Watersnakes consumed a variety of native fishes and amphibians. Invasion of Lake Erie by Round Gobies resulted in a dramatic change in watersnake diet to >90% Round Gobies, leading to increased watersnake growth rate, body size and size-specific fecundity (King et al., 2006a, 2008). Daily growth rates increased by 0.15 mm/day (erroneously reported as 0.44 mm/day in King et al., 2006a) and SVL increased by 6–9% after the Round Goby invasion (King et al., 2006a). Females now produce more offspring and female size now explains a greater proportion of the variation in offspring number. This increase in fecundity may be stimulating watersnake population growth since the Round Goby invasion (King et al., 2008).

In this paper, we examine the Round Goby–Lake Erie Watersnake interaction in more detail. We report rates of gastric digestion and maximum voluntary prey consumption among captive watersnakes. We also report on feeding frequency and location among free-ranging watersnakes. We use this information, together with information on snake energetics, to estimate potential individual and population-level impacts of watersnake predation on Round Gobies. Although our focus is on only a small portion of the geographic range of invasive Round Gobies, conspecific Northern Watersnakes are widely distributed in the Great Lakes region (Harding, 1997; Walley et al., in press) and are known to consume Round Gobies where they co-occur (J. Robinson, pers. comm.). Thus, our results should have applicability to a much larger geographic area. Our data on digestive rate and feeding frequency also provide an interesting comparison with similar investigations of other snakes, many of which are sit-and-wait predators that feed relatively infrequently and exhibit dramatic up-regulation in digestive physiology (Ott and Secor, 2007; Secor and Ott, 2007; Wilson, 2007). This contrasts with the foraging behavior of Lake Erie Watersnakes, and natricine snakes generally, which are active foragers and potentially feed quite frequently.

MATERIALS AND METHODS

Animal husbandry.—During the summers of 2006 and 2007, 41 adult, 15 juvenile, and seven neonate Lake Erie Watersnakes were captured from the Bass Islands in Lake Erie for use in feeding trials. Watersnakes were measured to determine snout–vent length (SVL) and mass, classified by sex, and individually marked with a PIT tag or by scale clipping. Adult male watersnakes ranged from 102–261 g, adult females ranged from 231–809 g, juveniles ranged from 30–80 g, and neonates ranged from 7–12 g. Adults were housed singly or in pairs in 37.8 L aquaria, juveniles were housed in groups of two or three in plastic sweater storage boxes, and neonates were housed in groups of up to five in shoe storage boxes. Housing containers were lined with cage paper, supplied with a water bowl and shelter, and held at near ambient summer temperatures in a large room open to the outdoors. Snakes were held without food for 48 hours before trials began to ensure no prey remained in the stomach prior to feeding trials.

Round Gobies were caught either by hook-and-line or trawling and placed according to size into 2000 L flow-through tanks in which water from Lake Erie was constantly circulated. Rocks and ceramic tiles placed in the tanks provided retreat sites. Due to their status as an invasive species in Ohio, Round Gobies not used in experiments were euthanized using MS222.

Rate of gastric digestion.—Adult and juveniles snakes were fed Round Gobies equal to 4.5–5.5% of snake body mass in their cages. Neonate snakes were fed Emerald Shiners (*Notropis atherinoides*) equal to 9.5–10.5% of their mass. Shiners were used because appropriately sized Round Gobies were not available. These meal sizes were derived from average meal size observed among wild-caught snakes (King, 1993; King et al., 1999; Jones, 2007). Once prey were consumed, snakes were transferred to a temperature-controlled cage where they remained for an allotted time interval after which they were manually regurgitated to recover prey remains. These remains were patted dry and weighed, and the proportion of mass digested was calculated from initial and final prey mass measurements. A single snake was used in a maximum of three trials with a minimum of 48 hr between trials after which snakes were released at their site of capture.

In order to determine the dependency of digestive rate on temperature, adult digestive rate trials were conducted at 25 and 30°C with time intervals of 4, 8, 12, and 16 hr. Juvenile and neonate watersnake digestive trials were conducted only at 30°C. Quadratic regression provided a consistently better fit than linear regression in characterizing the relationship between extent of gastric digestion and time. Regressions were forced through the origin to account for 0% prey digestion at time zero. Possible differences between males and females were tested using an overall test for coincidental regressions (Zar, 1999). When no difference was found, males and females were pooled. Following regression analysis, inverse prediction was used to determine time until 90% of prey mass was digested.

Maximum voluntary prey consumption.—Six adult females, five adult males, four juveniles, and four neonates were used in trials to determine the maximum amount of prey Lake Erie Watersnakes would voluntarily consume in a five-day period. During feeding trials, watersnakes were housed individually (adults in a 114 L aquarium, juveniles in a 40 L aquarium, and neonates in a shoe storage box). Cages contained a container of water with aerator and a shelter. A heat tape under one end of the cage provided a temperature gradient (ambient to 30°C). Three Round Gobies were placed in the water container, and the snake was allowed to feed freely for eight hours. The aquarium was checked every half hour and Round Gobies were replaced as necessary so that prey were available at all times. At the end of eight hours, remaining prey were removed and weighed. The total biomass consumed that day was calculated from the difference between prey mass available and prey mass remaining. This process was repeated for five consecutive days after which snakes were released at their site of capture. Individual prey equaled 3–7% of adult snake mass for adults, 3–15% of juvenile snake mass, and 15–45% of neonate snake mass.

Feeding frequency of free-ranging watersnakes.—Data on feeding frequency in free-ranging Lake Erie Watersnakes were collected during area-constrained searches performed from 2005–2007 (King et al., 2006b). Watersnakes were hand-captured, measured to obtain SVL and mass, classified

by sex, and palpated to detect recently consumed prey. One site, South Bass Island State Park (site 28 in fig. 2 of King et al., 2006a), was sampled throughout the active season in all three years. Sites on two other islands (Middle Bass Island, North Bass Island) were sampled throughout the active season in 2007 only. Log-linear analysis was used to test for independence among sex, time period, and feeding status. Time periods were initially defined as one-week intervals starting with the last week in May and ending with the first week in October. Successive weeks were then pooled to ensure there were at least ten captures per time period. Eleven time periods were defined in this manner: week 22, week 23, week 24, week 25, week 26, week 27, week 28, week 29, week 30, weeks 31–34, weeks 35–40. Subadults and adults were analyzed separately.

Feeding locations of free-ranging watersnakes.—Feeding location surveys were performed at three sites: South Bass Island State Park, Middle Bass Island–West End, and North Bass Island–South Shore (sites 28, 39, and 47 in fig. 2 of King et al., 2006b). For each survey, a boat was piloted to a point 300 m offshore and slow (<5 knots) passes were made parallel to shore, moving closer to shore with each pass. After reaching a depth of 1 m, the boat was piloted back to the 300 m offshore starting point. When a snake was observed, the boat was piloted as close as possible to the snake (1–5 m), and GPS coordinates (Raymarine C8 WAAS System), depth, and distance to shore (Bushnell laser rangefinder) were recorded. Surveys lasted one or two hours each and were performed between 0800 and 2100 hrs.

RESULTS

Rate of gastric digestion.—Fifty-seven digestive trials were completed with adult snakes (14 additional trials were omitted because of spontaneous regurgitation or an inability to recover any prey remains). There was a negative relationship between proportion of prey mass remaining and time which did not differ between males and females at 25°C ($F = 0.024$, $P = 0.98$) or 30°C ($F = 0.689$, $P = 0.51$) so sexes were pooled (Fig. 1; Table 1). Inverse prediction from the resulting regression relationship indicated that time until gastric digestion was 90% complete (10% of prey mass remained) was 20.1 hr at 25°C and 16.2 hr at 30°C. Twenty-five digestive trials were performed with juvenile watersnakes at 30°C (Fig. 1). The quadratic regression had a minimum at 15.3 hr at which time gastric digestion was 91% complete (Table 1; Fig. 1). However, the quadratic term was negative, resulting in an unrealistic increase in the amount of prey remaining beyond 15.3 hours (Fig. 1). Nine digestive rate trials were performed with neonate watersnakes. Quadratic regression results were similar to those of juvenile watersnakes with a minimum at 16.5 hr at which time gastric digestion was 87% complete (Table 1; Fig. 1).

Maximum voluntary prey consumption.—Nineteen maximum voluntary prey consumption trials were completed with six adult females, five adult males, four juveniles, and four neonates. The relative amount of Round Goby biomass consumed during the five-day trials varied between the age classes. Juveniles and neonates ate relatively large meals with juveniles consuming an average of 68.7% and neonates consuming on average 117.4% of their own body mass over five days (Table 2).

Adult males and females consumed relatively smaller amounts, averaging 39.2% and 30.0% of their own body mass, respectively (Table 2). Hence, mean prey biomass consumed as a percent of snake mass scaled as an inverse of snake size with neonates consuming the greatest percent per day and adult females consuming the least percent per day (Table 2). The number of meals eaten during the five-day trials did not vary greatly. On average, neonates, juveniles, and adult females ate approximately three days out of five, and adult males ate four days out of five (Table 2).

Feeding frequency of free-ranging watersnakes.—Recently consumed prey were detected in 348 of 2,910 adult watersnakes (79 of 1490 adult males, 269 of 1420 adult females) in 2005–2007. Log-linear analysis resulted in a most-parsimonious model that excluded the sex * time period * prey presence interaction but included all three two-way interactions ($G = 15.5$, df $= 10$, $P = 0.114$). Follow-up tests of independence showed all three of the two-way interactions to be significant, reflecting (1) a change in the frequency of sexes throughout the season (sex * time period interaction: $G = 378.7$, df $= 10$, $P < 0.001$), (2) a greater proportion of females with prey than males (sex * prey presence interaction: $G = 128.2$, df $= 1$, $P < 0.001$), and (3) a greater proportion of snakes with prey earlier in the season than later (time period * prey presence interaction: $G = 78.7$, df $= 10$, $P < 0.001$). Adult male watersnakes contained prey infrequently in late May and early June but increased thereafter, reaching a maximum of 16.7% in early July (Fig. 2). In contrast, adult female watersnakes contained prey from late May to early August with a maximum of 34.0% in early June (Fig. 2). Feeding frequencies for both sexes decreased to zero by the end of September (Fig. 2). Recently consumed prey were detected in 77 of 485 subadult watersnakes. In contrast to adults, loglinear analysis of subadult data offered no support for a difference in feeding frequency between the sexes (sex * prey presence interaction: $G = 0.207$, df $= 1$, $P = 0.649$). Feeding frequency of subadults did not remain constant throughout the active season (Fig. 2; time period * prey presence interaction: $G = 8.288$, df $= 3$, $P = 0.040$). However, data on subadults after the end of August are lacking. Using the proportion of snakes found to contain prey in each time period (Fig. 2) to generate season-long means, on average 11.6% of adult females, 6.9% of adult males, and 22.4% of subadults contained prey.

Feeding locations of free-ranging watersnakes.—One hundred thirty observations of foraging watersnakes were made during 12 separate surveys. The mean distance from shore among sites was 85.01 m (SD = 48.83). The mean water depth among sites was 3.32 m (SD = 1.35). There were just five observations (4%) of watersnakes at distances greater than 200 m from shore and just 16 observations (12%) at distances greater than 150 m (Fig. 3). The maximum distance observed was 229 m and this corresponded to the greatest water depth at 7.5 m (Fig. 3).

DISCUSSION

Gastric digestion and feeding frequency.—The digestive rate trials revealed (1) adult male and female Lake Erie Watersnakes have the same relative digestive rate despite their size differences, (2) a temperature difference of only five degrees
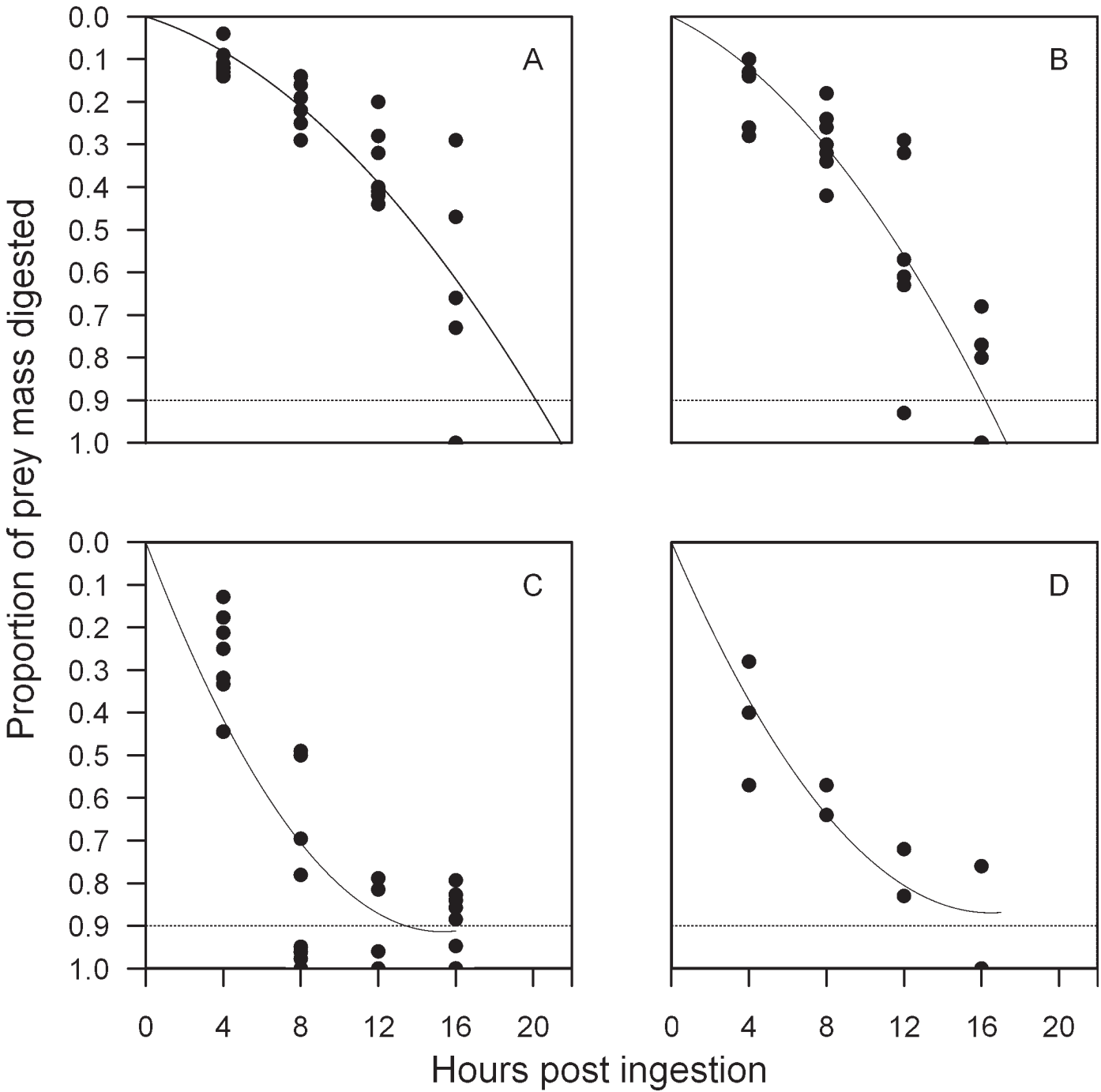
Fig. 1. Quadratic regression curves of digestive rate trials for adults at 25°C (A), adults at 30°C (B), neonates at 30°C (C), and juveniles at 30°C (D). Points represent individual trial values. The dashed line indicates the level at which 90% of prey mass was digested.

Table 1. Quadratic Regression Results of Digestive Rate Trials. Results include quadratic regression coefficients ($Y = b_1X + b_2X^2$), 95% confidence intervals of the coefficients, degrees of freedom, r^2 values, and P-values for the quadratic regression equations of adult Lake Erie Watersnakes at 25°C and 30°C, juvenile Lake Erie Watersnakes at 30°C, and neonate Lake Erie Watersnakes at 30°C.

Treatment	b_1	Lower 95% CI	Upper 95% CI	b_2	Lower 95% CI	Upper 95% CI	df1	df2	r^2	P
Adults–25°C	0.0145	−0.0046	0.0337	0.0015	0.0000	0.0029	2	24	0.895	<0.001
Adults–30°C	0.0215	0.0031	0.0399	0.0021	0.0008	0.0034	2	29	0.950	<0.001
Juveniles–30°C	0.1194	0.0963	0.1426	−0.0039	−0.0055	−0.0023	2	26	0.956	<0.001
Neonates–30°C	0.1055	0.0720	0.1390	−0.0032	−0.0057	−0.0008	2	7	0.978	<0.001

Table 2. Summary of Maximum Prey Consumption Trials for Neonates, Juveniles, Adult Males, and Adult Females. Average number of meals refers to the mean number of days on which snakes ate. The # of gobies, mass, and % of snake mass refer to the mean totals of the five-day trials for number of round gobies consumed, biomass of those round gobies, and the percent of snake mass that biomass represents, respectively. Percent of snake mass consumed per snake per day is the average percent of snake mass of round goby biomass each snake consumed per day.

| Group | Average number of meals | Five-day average totals | | | % of snake mass consumed per snake per day |
		# of gobies	mass	% of snake mass	
Neonates	2.8	4	8.6	117.4	23.5
Juveniles	3.2	12	23.6	68.7	13.7
Adult males	4.2	8	70.8	39.2	7.8
Adult females	2.8	5	151.4	30.0	6.0

has a significant impact on watersnake digestive rate, and (3) digestive rate of Lake Erie Watersnakes of all age classes is quite rapid. This last result is perhaps the most significant, especially when watersnakes are compared to non-natricine snakes. North American Rubber Boas digest less than half a mouse per day (mice were equal to 10–15% of snake body mass) at temperatures similar to those used in this study (Dorcas et al., 1997). Among four species classified as frequent feeders (Blue Racer, Kingsnake, Coachwhip, Bullsnake), the amount of prey remaining in the stomach exceeded 50% after one day and did not decrease to 10% or less until three or more days past ingestion (Secor and Diamond, 2000). Among four species classified as infrequent

feeders (North American Rosy Boa, Red-tailed Boa, Burmese Python, Sidewinder), the amount of prey remaining in the stomach approached or exceeded 75% after one day and did not decrease to 10% or less until six or more days (Secor and Diamond, 2000). In these studies, snakes were fed mammalian prey equaling 25% of snake mass whereas watersnakes were fed fish equaling 5% (juveniles, adults) or 10% (neonates) of snake mass. This difference in prey size and type may partly explain the higher rates of gastric digestion seen in watersnakes. However, meal sizes used in this study were typical of those recovered from free-ranging watersnakes. Furthermore, even if the time required for gastric digestion increased linearly with prey size (e.g., from 16 to 80 hr for prey equaling 5% vs. 25% of snake mass), watersnake digestive rates are rapid.

Subadult watersnakes appear to have even higher relative digestive rates than adults. Gastric digestion was 90% complete after approximately 16 hours in both neonates and adults, but neonates were fed prey equal to 10% of their body mass compared with 5% for adults. Gastric digestion
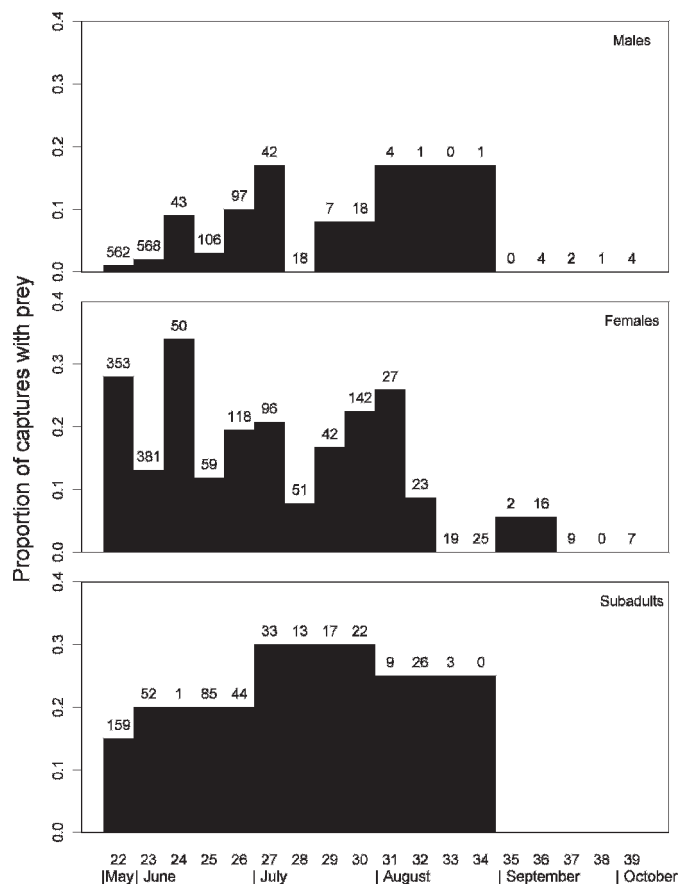

Fig. 2. Temporal patterns of feeding frequency among adult male, adult female, and subadult Lake Erie Watersnakes. Numbers on top of bars indicate the number of watersnake captures for each week. Numbers on the x-axis refer to weeks from January 1. To estimate season-long feeding frequency, weeks were pooled as indicated by blocks of weeks with the same proportions.
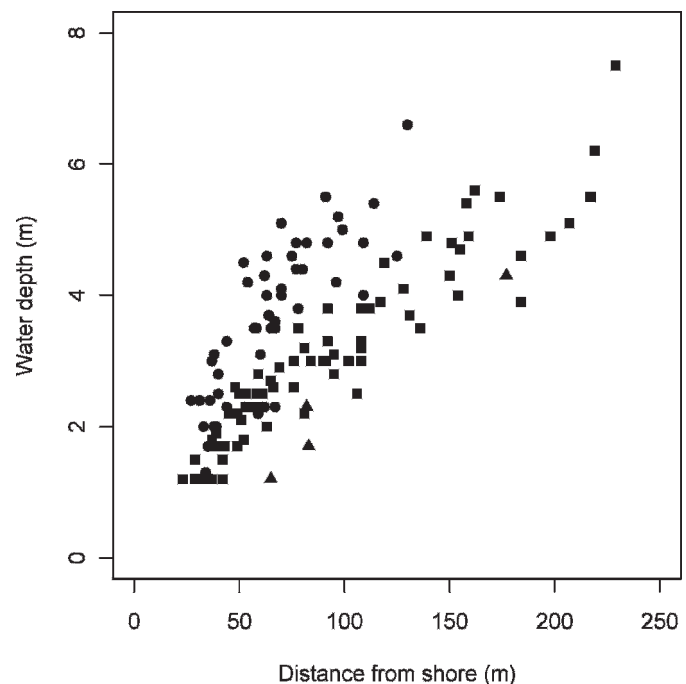

Fig. 3. Distribution of watersnake foraging locations by water depth and distance from shore. Circles represent observations at South Bass Island State Park, squares represent observations at Middle Bass Island–West End, and triangles represent observations at North Bass Island–South Shore.

was 90% complete in approximately 15 hours among juveniles fed prey equal to 5% of their body mass. The reason for this difference is unclear but may relate to the greater surface area to volume ratio of small vs. large prey. If so, watersnakes might voluntarily consume prey that are smaller than the maximum size imposed by gape limitation to facilitate rapid digestion and rapid energy assimilation (King, 2002).

Feeding frequency in watersnakes also appears higher than in many other species. Secor and Diamond (2000) reported the feeding intervals for the eight snake species used in their analyses. The Blue Racer had the lowest interval at eight days, and the Burmese Python had the highest interval at 40 days (Secor and Diamond, 2000). From our season-long feeding frequency dataset, we found on that on average 6.9% of adult males and 11.6% of adult females contained prey. Given that our digestive rate trials indicate that prey remain detectable for as little as 16 hrs post-ingestion, watersnake feeding intervals likely average 6–9 days and may be markedly shorter during periods of peak foraging (e.g., June and July). The maximum prey consumption trials give further support to the conclusion that feeding frequency is high in Lake Erie Watersnakes. Watersnakes typically ate on three or four of the five days they were offered food.

The occurrence of prey items in the digestive tract of snakes is highly variable, ranging from less than 10% (adult male Lake Erie watersnakes, this study) to 96% (*Tantilla gracilis*, Cobb, 2004). Among previous studies of natricines, the proportion of animals containing prey ranges from 26% to 71% (Mushinsky and Hebrard, 1977; Seigel, 1992; Aldridge and Bufalino, 2003; Andreadis, 2007). Other piscivorous species include *Acrochordus arafurae* and *Cerberus rynchops*, for which 10% and 30% contained prey (Jayne et al., 1988; Houston and Shine, 1993). Compared with these studies, adult Lake Erie Watersnakes have a relatively low occurrence of prey items (6.9% for males, 11.6% for females). Prey type and temperature likely contribute to this variation, affecting both feeding frequency (Naulleau, 1983) and digestive rate (this study). Method of prey detection (palpation, manual regurgitation, dissection) is also a factor. While these sources of variation may limit comparisons among studies, the large sample size obtained in this study allows for meaningful comparisons of relative feeding frequency among sex and age classes and over time even if knowledge of absolute feeding frequency is incomplete.

Experiments investigating gastric digestion and prey consumption in the Northern Watersnake, *Nerodia sipedon sipedon*, similar to those reported here, were performed by Brown (1958). Northern Watersnakes fed frogs weighing 16–38% (mean of 28%) of snake mass completed gastric digestion in 42–66 hr (mean of 50.4 hr) at 24°C. Thus, Northern Watersnakes took about three times longer to digest a meal three times larger than that used in our experiments. In maximum prey consumption experiments, adult Northern Watersnakes ate 38–50% (mean of 43%) of their own body mass per week. Extrapolation from our five-day tests yields maximum consumption of about 42% of adult snake body mass per week in Lake Erie watersnakes.

Patterns of prey consumption in free-ranging watersnakes are consistent with many aspects of their life history. Among adults, females are more likely to contain prey than males as might be expected given the larger body size of females and their large commitment of energy to reproduction (King, 1986; Peterson et al., 1998; Beaupre and Duvall, 1998; Ladyman et al., 2003). More frequent feeding by females may also contribute to phenotypic plasticity of watersnake head dimensions, resulting in greater relative head size compared to males (Queral-Regil and King, 1998). Adult males are less likely to contain prey in May and early June, while they are active in courtship and mating, than later in the active season, a pattern also seen in gartersnakes (O'Donnell et al., 2004). In contrast, feeding by adult females remains high throughout the spring and summer and only decreases in late August with the approach of parturition as has been reported in other natricines (Gregory et al., 1999; but see Aldridge and Bufalino, 2003). Subadults feed frequently throughout spring and summer with no difference between the sexes. This may benefit subadults by promoting rapid growth, allowing them to more quickly outgrow potential predators and reach reproductive maturity.

Implications for Round Gobies.—To determine potential annual consumption of Round Gobies by Lake Erie Watersnakes, we explore four different scenarios. In all scenarios, we assume that the active season for watersnakes lasts 133 days (15 May–25 September), the adult U.S. Lake Erie Watersnake population is approximately 12,000 (R. B. King, unpubl.), adult watersnakes average 171 g (males) and 540 g (females), and the sex ratio of adults is 1:1. In scenario one, we use our digestive rate data and assume that watersnakes digest one average-sized (5% of snake mass) Round Goby every 17 hours (90% digestion at 30°C trials in 16 hr plus one hr to reach 100% digestion), or 1.4 Round Gobies per day. In scenario two, we use our maximum prey consumption observations and assume that watersnakes consume 7.8% (adult males) or 6.0% (adult females) of their body mass every day. In scenario three, we use the season-long average proportions of free-ranging snakes found to contain prey (6.9% for adult males, 11.6% for adult females) and assume that prey remain detectable for 16 hr. In scenario four, we combine the estimated energy assimilation rate (kJ/day) for another natricine, the Common Gartersnake (*Thamnophis sirtalis*), $0.414 * \text{snake mass}^{0.95}$ (Peterson et al., 1998), the energy density of Round Gobies (J•g wet mass^{-1}), $2942.86 * \text{Round Goby mass}^{0.08646}$ (Bunnell et al., 2005), and the assimilation efficiency for the Wandering Gartersnake, *Thamnophis elegans*, when eating fish of 0.812 (Britt et al., 2006).

Projected Round Goby consumption is similar among scenarios one, two and four (ranging from 2.2 to 3.3 million fish or 36,499 to 56,178 kg per yr) but is an order of magnitude lower under scenario three (0.2 million fish or 4,455 kg per year; Table 3). Discrepancies among these scenarios are not entirely surprising. Scenarios one and two likely represent an upper limit to Lake Erie Watersnake prey consumption because they are based on maximum digestion rate and maximum voluntary consumption. In contrast, observed proportions of snakes containing prey (scenario three) may underestimate feeding frequency because some prey go undetected and because snake behavior may change with feeding status (e.g., snakes that have fed recently may be more secretive and less likely to be captured). In addition, the scaling of energy assimilation rate as a function of body size may differ between gartersnakes (which weighed 70 g or less, Peterson et al.,

Table 3. Summary of Consumption Rates of Round Gobies by Lake Erie Watersnakes under Four Scenarios. Each scenario is based upon a different set of parameters as given. Rates are split between the sexes when necessary. All rates are based on a 133 day active season and a watersnake population size of 12,000 with a 1:1 sex ratio.

	Based upon	Rate (male/female)	g of goby/snake/day (male/female)	kg of goby/snake/year (male/female)	Biomass of round goby consumed per year
Scenario 1	experimental digestive rate	1.4 round gobies per day	12.1/38.1	1.6/5.1	40,051
Scenario 2	max. prey consumption	7.8%/6.0% of snake mass per day	13.3/32.4	1.8/4.3	36,499
Scenario 3	free-ranging feeding frequency	6.9%/11.6% snakes feeding per day	0.9/4.7	0.12/0.62	4,455
Scenario 4	physiological parameters	65.2/176.2 kJ required per day	19.0/51.4	2.5/6.8	56,178

1998) and watersnakes in which adult males average 171 g and adult females average 540 g (scenario four). Finally, all four scenarios are incomplete because they include only adult watersnakes, a necessity arising from a lack of population estimates for younger age classes.

Despite their uncertainty, these projections are useful in assessing the degree to which Lake Erie Watersnakes might impact Round Goby populations. In the broadest sense, it is apparent that even frequent predation by Lake Erie Watersnake is unlikely to have a significant impact on the estimated 9.9 billion Round Gobies residing in the western basin of Lake Erie (Johnson et al., 2005). However, given that watersnake foraging is concentrated within about 230 m of shore, predation might have local effects on Round Goby populations. These effects could be magnified by the nest guarding behavior of male Round Gobies, which may increase their vulnerability to watersnakes that forage by probing rock crevices and cavities (Brown, 1958; Miller, 1986). When nest-guarding males are removed, juveniles arrive quickly and consume the unguarded eggs (Wickett and Corkum, 1998), thus reducing Round Goby reproductive success. Such local effects may benefit native fish species by reducing egg predation and competition such as seen with the Smallmouth Bass (Steinhart et al., 2004). The U.S. islands in Lake Erie include about 64 km of shoreline, giving Lake Erie Watersnakes a foraging area of about 15 km² (0.2% of the area of Lake Erie's western basin). However, local effects might be expected within the nearshore waters of the Great Lakes more generally due to predation by Northern Watersnakes outside of the Lake Erie island region. The magnitude of any local effects of watersnake predation depends on spatial and temporal patterns of Round Goby dispersal. Unfortunately, at present these patterns are unknown.

The degree to which Round Goby populations are still increasing is also an unknown, although there is some evidence that numbers in the central basin of Lake Erie are stable or decreasing (Bunnell et al., 2005). Round Goby population growth and the effects this invasion has had on Lake Erie Watersnake diet and life history (King et al., 2006b, 2008) illustrate the rapidity and extent to which invasive species can impact natural populations and communities. Further changes may become evident over time. For example, the Lake Erie Watersnake–Round Gobies interaction may result in new patterns of natural selection on snake and fish morphology and behavior. Invasive species continue to cause unpredictable effects on native species much like

the ones affecting Lake Erie Watersnakes. Further research into the Lake Erie Watersnake–Round Goby relationship could bring illumination to other invasive species systems.

LITERATURE CITED

Aldridge, R. D., and A. P. Bufalino. 2003. Reproductive female common watersnakes (*Nerodia sipedon sipedon*) are not anorexic in the wild. Journal of Herpetology 37:416–419.

Andreadis, P. T. 2007. Control of food intake and expression of hunger in the northern water snake, *Nerodia sipedon* (L.). Unpubl. M.S. thesis, University of Tennessee, Knoxville, Tennessee.

Beaupre, S. J., and D. Duvall. 1998. Variation in oxygen consumption of the western diamondback rattlesnake (*Crotalus atrox*): implications for sexual size dimorphism. Journal of Comparative Physiological Biology 168:497–506.

Britt, E. J., J. W. Hicks, and A. F. Bennett. 2006. The energetic consequences of dietary specialization in populations of the garter snake, *Thamnophis elegans*. The Journal of Experimental Biology 209:3164–3169.

Brown, E. E. 1958. Feeding habits of the northern water snake, *Natrix sipedon sipedon* L. Zoologica 43:55–71.

Bunnell, D. B., T. B. Johnson, and C. T. Knight. 2005. The impact of introduced round gobies (*Neogobius melanostomus*) on phosphorus cycling in central Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 62:15–29.

Caldow, R. W. G., R. A. Stillman, S. E. A. L. V. D. Duvell, A. D. West, S. McGrorty, J. D. Goss-Custard, P. J. Wood, and J. Humphreys. 2007. Benefits to shorebirds from

invasion of a non-native shellfish. Proceedings of the Royal Society B 274:1449–1455.

Charlebois, P. M., E. J. Marsden, R. G. Goettel, R. K. Wolfe, D. J. Jude, and S. Rudnika. 1997. The round goby, *Neogobius melanostomus* (Pallas): a review of European and North American literature. Illinois–Indiana Sea Grant Program, Urbana, and Illinois Natural History Survey, Champaign.

Cobb, V. A. 2004. Diet and prey size of the flathead snake, *Tantila gracilis*. Copeia 2004:397–402.

Conant, R., and W. Clay. 1937. A new subspecies of watersnake from the islands in Lake Erie. Occassional Papers of the University of Michigan Museum of Zoology 346:1–9.

Dorcas, M. E., C. R. Peterson, and M. E. T. Flint. 1997. The thermal biology of digestion in rubber boas (*Charina bottae*): physiology, behavior, and environmental constraints. Physiological Zoology 70:292–300.

Fazio, B. B., and J. Szymanksi. 1999. Endangered and threatened wildlife and plants; threatened status for Lake Erie water snakes (*Nerodia sipedon insularum*) on the offshore islands of Western Lake Erie. Federal Register 64:47126–47134.

Gregory, P. G., L. H. Crampton, and K. M. Skebo. 1999. Conflicts and interactions among reproduction, thermoregulation and feeding in viviparous reptiles: Are gravid females anorexic? Journal of Zoology (London) 248:231–241.

Harding, J. H. 1997. Northern water snake, p. 252–256. *In*: Amphibians and Reptiles of the Great Lakes Region. The University of Michigan Press, Ann Arbor, Michigan.

Houston, D., and R. Shine. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. Journal of Animal Ecology 62:737–748.

Janssen, J., and D. J. Jude. 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. Journal of Great Lakes Research 27:319–328.

Jayne, B. C., H. K. Voris, and K. B. Heang. 1988. Diet, feeding behavior, growth, and numbers of a population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia. Fieldiana: Zoology 50:1–14.

Johnson, T. B., M. Allen, L. D. Corkum, and V. A. Lee. 2005. Comparison of methods needed to estimate population size of round gobies (*Neogobius melanostomus*) in Western Lake Erie. Journal of Great Lake Research 31:78–86.

Jones, P. C. 2007. Rapid prey consumption and digestion by the Lake Erie watersnake: implications for an invasive prey species. Unpubl. M.S. thesis, Northern Illinois University, DeKalb, Illinois.

Jude, D. J. 1997. Round gobies: cyberfish of the third millennium. Great Lakes Research Review 3:27–34.

King, R. B. 1986. Population ecology of the Lake Erie water snake, *Nerodia sipedon insularum*. Copeia 1986:757–772.

King, R. B. 1993. Microgeographic, historical, and size-correlated variation in water snake diet composition. Journal of Herpetology 27:90–94.

King, R. B. 2002. Predicted and observed maximum prey size–snake size allometry. Functional Ecology 16:766–772.

King, R. B., A. Queral-Regil, T. D. Bittner, and J. M. Kerfin. 1999. *Nerodia sipedon insularum*. Herpetological Review 30:169–170.

King, R. B., A. Queral-Regil, and K. M. Stanford. 2006a. Population size and recovery criteria of the threatened Lake Erie watersnake: integrating multiple methods of population estimation. Herpetological Monographs 20:83–104.

King, R. B., J. M. Ray, and K. M. Stanford. 2006b. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. Canadian Journal of Zoology 84:108–115.

King, R. B., K. M. Stanford, and J. M. Ray. 2008. Reproductive consequences of a changing prey base in island watersnakes. South American Journal of Herpetology 3:155–161.

Kovtun, I. F. 1977. On the fecundity of the round goby, *Gobius melanostomus*, from the Sea of Azov. Journal of Icthyology 19:161–193.

Ladyman, M., X. Bonnet, O. Lourdais, D. Bradshaw, and G. Naulleau. 2003. Gestation, thermoregulation, and metabolism in a viviparous snake, *Vipera aspis*: evidence for fecundity-independent costs. Physiological and Biochemical Zoology 76:497–510.

MacInnis, A. J., and L. D. Corkum. 2000a. Fecundity and reproductive season of the round goby *Neogobius melanostomus* in the upper Detroit River. Transactions of the American Fisheries Society 129:136–144.

MacInnis, A. J., and L. D. Corkum. 2000b. Age and growth of round goby *Neogobius melanostomus* in the Upper Detroit River. Transactions of the American Fisheries Society 129:852–858.

Miller, P. J. 1986. Gobiidae, p. 1019–1085. *In*: Fishes of the Northeastern Atlantic and the Mediterranean. P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielson, and E. Tortonese (eds.). UNESCO, Paris.

Mooney, H., R. Mack, and J. A. McNeely (eds.). 2005. Invasive Alien Species: A New Synthesis. Island Press, Washington, D.C.

Mushinsky, H. R., and J. J. Hebrard. 1977. Food partitioning by five species of water snakes in Louisiana. Herpetologica 33:162–166.

Naulleau, G. 1983. The effects of temperature on digestion in *Vipera aspis*. Journal of Herpetology 17:166–170.

O'Donnell, R. P., R. Shine, and R. T. Mason. 2004. Seasonal anorexia in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. Behavioral Ecology and Sociobiology 56:413–419.

Ott, B. D., and S. M. Secor. 2007. The specific dynamic action in boas and pythons, p. 299–310. *In*: The Biology of the Boas and Pythons. R. W. Henderson and R. Powell (eds.). Eagle Mountain Publishing, LC, Eagle Mountain, Utah.

Peterson, C. C., B. M. Walton, and A. F. Bennett. 1998. Intrapopulation variation in ecological energetics of the garter snake *Thamnophis sirtalis*, with analysis of precision of doubly labeled water measurements. Physiological Zoology 71:333–349.

Phillips, B. L., G. P. Brown, and R. Shine. 2003. Assessing the potential impact of cane toads on Australian snakes. Conservation Biology 17:1738–1747.

Phillips, B. L., and R. Shine. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. Proceedings of the National Academy of Sciences of the United States of America 101:17150–17155.

Phillips, B. L., and R. Shine. 2006. Allometry and selection in a novel predator–prey system: Australian snakes and the invading cane toad. Oikos 112:122–130.

Pimental, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Queral-Regil, A., and R. B. King. 1998. Evidence for phenotypic plasticity in snake body size and relative head dimensions in response to amount and size of prey. Copeia 1998:423–429.

Ray, W. J., and L. D. Corkum. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. Environmental Biology of Fishes 50:267–273.

Roemer, G. W., C. J. Bonlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proceedings of the National Academy of Sciences of the United States of America 99:791–796.

Secor, S. M., and J. M. Diamond. 2000. Evolution of regulatory responses to feeding in snakes. Physiological and Biochemical Zoology 73:123–141.

Secor, S. M., and B. D. Ott. 2007. Adaptive correlation between feeding habits and digestive physiology for boas and pythons, p. 257–268. *In*: Biology of the Boas and Pythons. R. W. Henderson and R. Powell (eds.). Eagle Mountain Publishing, LC, Eagle Mountain, Utah.

Seigel, R. A. 1992. Ecology of a specialized predator: *Regina grahami* in Missouri. Journal of Herpetology 26:32–37.

Steinhart, G. B., E. A. Marschall, and R. A. Stein. 2004. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. Transactions of the American Fishieries Society 133: 121–131.

Walley, H. D., R. B. King, J. M. Ray, and T. L. Wusterbarth. In press. *Nerodia sipedon* (Linnaeus) Northern Watersnake. Catalogue of American Amphibians and Reptiles.

Wickett, R. G., and L. D. Corkum. 1998. You have to get wet: a case study of the nonindigenous Great Lakes fish, round goby. Fisheries 23:26–27.

Wilson, D. 2007. Foraging ecology and diet of an ambush predator: the green python (*Morelia viridis*), p. 141–149. *In*: Biology of the Boas and Pythons. R. W. Henderson and R. Powell (eds.). Eagle Mountain Publishing, LC, Eagle Mountain, Utah.

Zar, J. 1999. Biostatistical Analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey.