

REPRODUCTIVE CONSEQUENCES OF A CHANGING PREY BASE IN ISLAND WATERSNAKES (REPTILIA: COLUBRIDAE)

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ABSTRACT. Island populations of the Lake Erie watersnake (*Nerodia sipedon insularum*) have experienced a dramatic environmental change in the form of a new abundant prey species, the round goby (*Neogobius melanostomus*). Effects of this biotic change on watersnake reproductive characteristics were tested by comparing offspring size and the relationship between female size and offspring number before and after the round goby invasion. Offspring number, but not offspring size, increased as a consequence of watersnake diet change. In addition, female size explained a greater proportion of the variation in offspring number following the round goby invasion (60% vs. 25%). The combined effects of increased female size and offspring number are projected to result in an increase in watersnake fecundity exceeding 25% and may be stimulating watersnake population growth since the round goby invasion. The rapidity of watersnake diet change and consequent change in fecundity is consistent with the maximization hypothesis of life history theory and suggests that watersnake life history may have been more strongly limited by resource availability prior to the round goby invasion.

KEYWORDS. diet change, invasive species, Lake Erie watersnake, *Nerodia sipedon*, reproductive allometry, round goby.

INTRODUCTION

Island biotas can be especially sensitive to environmental change. This sensitivity arises from the fact that island populations are typically smaller and island communities are often simpler in structure than are mainland populations and communities. As a consequence, island biotas are particularly vulnerable to such threats as overexploitation; introduced predators, competitors, and pathogens; habitat loss and degradation; and climate change. Because islands exhibit high levels of endemism, they are often a priority for conservation. And because they are physically bounded, islands provide useful natural laboratories for studying the mechanisms by which environmental change affects populations (e.g., Aubret *et al.*, 2004).

The Lake Erie watersnake, *Nerodia sipedon insularum* (Serpentes, Colubridae, Natricinae), is an endemic subspecies restricted to the island region of Lake Erie (Conant and Clay, 1937), the most southern of the North American Great Lakes. The island region straddles the U.S. – Canadian border and includes about 20 islands that range in size from < 1 to > 4,000 ha and are < 1 to 22 km from the mainland (King *et al.*, 2006b: fig. 1). Lake Erie watersnakes are highly variable in color pattern and island populations include high frequencies of unpatterned and reduced-pattern morphs absent from mainland populations of regularly patterned (banded) Northern watersnakes

(*N. s. sipedon*). This difference in color pattern is the result of a dynamic balance between natural selection and gene flow (King and Lawson, 1995, 1997; Ray and King, 2006). Visual predators impose selection favoring unpatterned snakes along the exposed limestone and dolomite shorelines of islands. In contrast, regularly patterned morphs are favored in more densely vegetated mainland habitats. However, the islands are incompletely isolated and gene flow between the mainland and the islands is responsible for the persistence of regularly patterned morphs in island populations (King and Lawson, 1995).

Lake Erie watersnakes are listed as threatened in the U.S. and endangered in Canada, Ontario, and Ohio (Fazio and Szymanski, 1999). The rationale for protection includes restricted geographic distribution (the island region occupies an area < 40 km in diameter and includes just 105 km of shoreline habitat) and a history of population decline. Recovery actions include long-term monitoring and research, habitat protection and management, and public outreach aimed at reducing human-caused mortality (United States Fish and Wildlife Service, 2003; King *et al.*, 2006b).

The North American Great Lakes have been impacted by a large number of invasive aquatic species (Stewart *et al.*, 1998; Ricciardi and MacIssac, 2000; Ricciardi, 2001). One recent invader is the round goby, *Neogobius melanostomus* (Marsden and Jude, 1995; Jude, 1997; Corkum *et al.*, 2004). This fish was

first documented in Lake Erie in 1993 and increased rapidly in number, reaching an estimated population of nearly 10 billion in the western basin of Lake Erie by 2004 (Johnson *et al.*, 2005). Round gobies feed on zebra and quagga mussels, two other aquatic invasive species (Ray and Corkum, 1997). They also feed on the eggs and fry of native fishes and compete for both food and space (French and Jude, 2001; Janssen and Jude, 2001; Steinhart *et al.*, 2004)

Life history theory suggests several hypotheses regarding how resource availability may affect reproductive characteristics (Roff, 2002; Stearns, 1992). The maximization (or constraint) hypothesis posits that growth rate and reproductive allocation are environmentally determined. Hence, the marked increase in prey abundance that has resulted from the round goby invasion (Bunnell *et al.*, 2005; Johnson *et al.*, 2005) is predicted to result in increased female watersnake growth and increased offspring size or number. Alternatively, the optimization hypothesis posits that observed suites of life history characteristics are the result of intrinsic trade-offs (e.g., between reproductive allocation and female survival). As a consequence, changes in resource availability are expected to have only small effects on life history traits over the short-term, although adaptive genetic changes may be observed over a longer period (e.g. Bonnet *et al.*, 2000).

Evidence for effects of resource availability on snake life history comes from both laboratory experiments and field observations. Experimental manipulations of resource availability resulted in changes in offspring number but not offspring size in both oviparous species (*Elaphe guttata*) and viviparous species (*Thamnophis marcianus*, *Nerodia sipedon*) (Ford and Seigel, 1989; Seigel and Ford, 1991, 2001; Barron and Andraso, 2001). In the field, annual variation in food availability affected the relationship between female size and offspring number in water pythons (*Liasis fuscus*) and keelbacks (*Tropidonophis mairii*) (Shine and Madsen, 1997; Madsen and Shine, 1999; Brown and Shine, 2007). In northern California populations of the wandering gartersnake (*Thamnophis elegans*), spatial variation in resource availability influenced multiple aspects of life history (Bronikowski and Arnold, 1999; Bronikowski, 2000). In three lakeshore *T. elegans* populations where prey and water are continuously available, snakes grow rapidly, mature quickly, and have low survival as adults; there is a significant positive relationship between female snout-vent length (SVL) and offspring number. In three nearby meadow populations where prey

and water availability are more variable, snakes grow more slowly, mature later, and have higher survival as adults; there is no significant relationship between female SVL and offspring number (Bronikowski and Arnold, 1999).

The abundance of round gobies in Lake Erie has resulted in a dramatic shift in watersnake diet, with round gobies now comprising > 90% of prey consumed (King *et al.*, 2006a). This has led to increased watersnake growth rates and body size and, based on the relationship between female size and offspring number prior to the round goby invasion, a predicted increase in female fecundity (King *et al.*, 2006a). In this paper, we test this prediction by comparing female watersnake reproductive characteristics before and after the round goby invasion. Lake Erie watersnakes provide an interesting contrast to previous studies of the effects of resource availability on snake life history described above. In watersnakes, variation in resource availability is the result of a diet change following establishment of an invasive species rather than annual variation (water pythons, keelbacks) or spatial variation (gartersnakes) in native prey. Furthermore, the rapidity with which watersnake diet has changed (King *et al.*, 2006a) makes this case especially timely as evolutionary ecologists strive to understand and predict how organisms may respond to environmental change.

MATERIAL AND METHODS

Data on Lake Erie watersnake reproductive characteristics were collected before (n = 36 females and their young from 1979-1990) and after (n = 62 females and their young from 2003-2005) the round goby invasion (Table 1). Females were captured by hand and maintained in captivity until parturition.

TABLE 1. Sample sizes (number of females and litters) upon which comparisons of reproductive parameters before and after the round goby invasion are based.

	Year	N		Total
Pre-Round Goby Invasion	1979	2	}	36
	1981	9		
	1982	6		
	1983	16		
	1990	3		
Post-Round Goby Invasion	2003	40	}	62
	2004	18		
	2005	4		

Females were housed singly or in pairs within 40 l aquaria lined with paper. A heat tape under one end of the aquaria provided a thermal gradient. Fresh water was available *ad libitum* and a ceramic tile or plastic shelter was available into which snakes could retreat. Within two days following parturition, females were measured to obtain post-partum mass and snout-vent length (SVL). All live- and still-born offspring were counted, classified by sex by everting hemipenes or probing (Fitch, 1987) and measured to obtain mass (0.1 g) and SVL (mm). Females and offspring were released at the female's site of capture soon after parturition. Nine females captured in 2003 were recaptured in 2004 ($n = 8$) and 2005 ($n = 1$). To avoid pseudoreplication and to reduce differences in sample size among years, only data from the second capture of these females were used. Data obtained were used to compare (1) the relationship between female SVL and offspring number and (2) offspring size before and after the round goby invasion.

A two-part analysis of covariance (ANCOVA) was used to test for differences in the relationship between female size and number of offspring with offspring number (sum of live- and still-born) as the dependent variable, time (pre- vs. post-round goby invasion) as the factor, and female SVL as the covariate. First, the significance of the time-by-female SVL interaction was tested to determine if the slope of the relationship

differed before and after the round goby invasion. When this interaction was found to be non-significant (see Results), a second ANCOVA was conducted, with the time-by-female SVL interaction omitted, to test if elevations (intercepts) differed before and after the round goby invasion. In addition, correlation coefficients between female SVL and offspring number were compared using a t-test (Sokal and Rohlf, 1994, p. 582). Both offspring number and female SVL were transformed using natural logarithms prior to analysis (King, 2000). Possible differences in offspring size before and after the round goby invasion were tested by computing the mean mass of live offspring for each litter and then comparing litter means using a t-test. A significance level of 0.05 was used in all analyses.

RESULTS

The test for a difference in the slope of the relationship between female SVL and offspring number before and after the round goby invasion approached significance (ANCOVA, time-by-female SVL interaction: $F_{1,94} = 3.23$, $P = 0.076$; Fig. 1A). The test for a difference in elevation in this relationship was significant (effect of time: $F_{1,95} = 5.27$, $P = 0.024$) with offspring numbers in the post round goby invasion

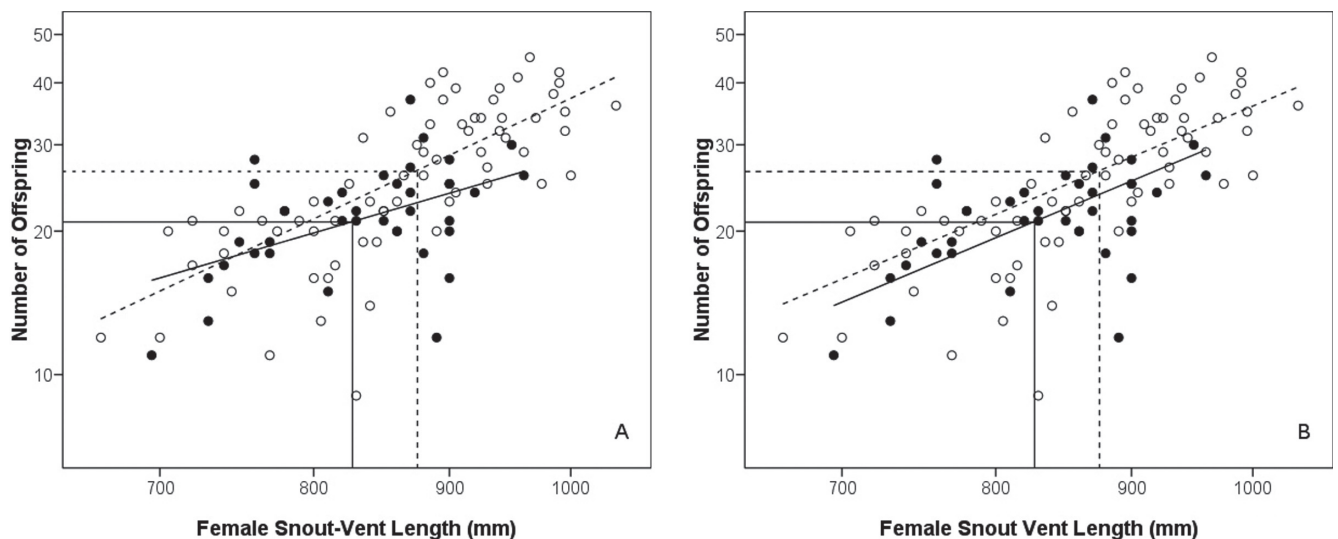


FIGURE 1. Relationship between female SVL and offspring number in Lake Erie watersnakes before (filled circles, solid line) and after (open circles, dashed line) the round goby invasion. Vertical and horizontal lines represent mean female SVL and expected offspring number before (solid) and after (dashed) the round goby invasion. Although the difference in slopes only approaches significance ($P = 0.076$), regression lines using separate slope estimates are shown in A for heuristic purposes (see Discussion); regression lines using the pooled slope estimate are shown in B. Regression equations in A before round goby invasion: $\ln(N) = -7.68 + 1.60\ln(\text{SVL})$; after round goby invasion: $\ln(N) = -13.99 + 2.55\ln(\text{SVL})$. Regression equations in B before the round goby invasion: $\ln(N) = -12.31 + 2.29\ln(\text{SVL})$; after the round goby invasion: $\ln(N) = -12.20 + 2.29\ln(\text{SVL})$.

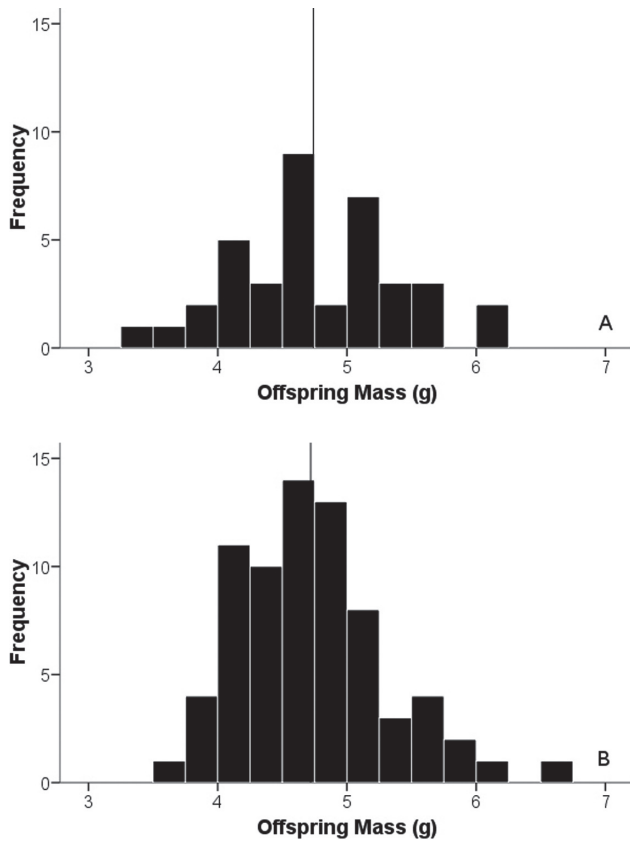


FIGURE 2. Frequency histograms of mean litter mass before (A) and after (B) the round goby invasion. Overall means are indicated by vertical reference lines.

sample exceeding those in the pre round goby invasion sample (Fig. 1B). Furthermore, the correlation between female SVL and offspring number in the post round goby invasion sample exceeded that in the pre round goby invasion sample ($r = 0.77$ vs. 0.50 , $t = 2.25$, $P = 0.012$). Female SVL explained just 25% of the variation in offspring number in the sample taken before the round goby invasion compared to 60% in the post-invasion sample. Offspring mass (mean of litter means) averaged 4.72 g (range = 3.47–6.13 g) in the pre-invasion sample and 4.74 g (3.70–6.57 g) in the post-invasion sample. This difference was not significant ($t = 0.19$, $P = 0.853$; Fig. 2).

DISCUSSION

Invasion of Lake Erie by round gobies has resulted in a dramatic change in watersnake diet, leading to increased watersnake growth rate, body size, and size-specific fecundity (King *et al.*, 2006a; this study). Females now produce more offspring and female size now explains a greater proportion of the variation in

offspring number; that is, offspring number is more tightly correlated with female SVL. In contrast, offspring size has remained unchanged following the round goby invasion.

Previously, King *et al.* (2006a) predicted that increased female body size (from a mean of 827 to 875 mm SVL) should result in an increase in mean watersnake fecundity of about 9% following the round goby invasion. However, this prediction was based solely on the increase in female SVL seen following the round goby invasion and assumed that the relationship between female size and offspring number had remained unchanged. Incorporating the upward shift in the relationship between female SVL and offspring number reported here results in an even greater effect on female fecundity. Prior to the round goby invasion, a female of average size (827 mm SVL) would have been expected to produce 20.9 offspring; following the round goby invasion, a female of average size (875 mm SVL) would be expected to produce 26.5 offspring, an increase of more than 25% (Fig. 1B). Given that the test for a difference in slope in the relationship between offspring number and female size approached significance ($P = 0.076$), it is noteworthy that a similar increase in fecundity is predicted when separate slope estimates are used (20.9 vs. 26.5 offspring; Fig. 1A). Such an increase in fecundity may be stimulating watersnake population growth since the round goby invasion (R. B. King and K. M. Stanford, unpublished data), an example of facilitation of a native species by an invasive species (Rodriguez, 2006).

In Lake Erie watersnakes diet change and associated changes in life history (increased growth rate, adult body size, and female fecundity) have occurred in as little as 10 years (three or fewer watersnake generations). The rapidity of these changes makes it unlikely that they represent evolved responses to natural selection, but rather suggests that some watersnake life history characters are relatively plastic. Such plasticity is consistent with the maximization hypothesis of life history theory and suggests that watersnake life history may have been more strongly limited by resource availability prior to the round goby invasion than is the case now. The lack of change in offspring mass indicates that not all life history traits are plastic. Unfortunately, data are currently lacking for other Lake Erie watersnake life history traits, including survivorship and age at maturity, which may also be affected by resource availability.

Patterns of life history variation in northern California populations of the wandering gartersnake, *T. elegans*, suggest a role for both optimization and

maximization in the face of resource variability (Bronikowski 2000, Bronikowski and Arnold 1999). Common garden experiments demonstrate that variation in growth rate has a genetic basis. In addition, clear trade-offs exist among growth, survival, and reproduction. These observations are consistent with the optimization hypothesis. However, one meadow population of *T. elegans* that recently experienced an increase in prey availability, has responded with increased growth and fecundity (like that of lakeshore populations of *T. elegans* and Lake Erie watersnakes), as expected under the maximization hypothesis. Maximization is also evident in patterns of annual variation in offspring number in water pythons and keelbacks in response to changing prey availability (Shine and Madsen, 1997; Madsen and Shine, 1999; Brown and Shine, 2007).

Plasticity in offspring number in response to resource availability may be widespread among snakes and could underlie the great variation observed in the strength of the relationship between female SVL and offspring number. Such variation is evident in Seigel and Ford's (1987) review of snake reproduction. Among 61 data sets representing 48 species (Seigel and Ford, 1987: table 8-2), female SVL explained from 0-98% of the variation in offspring number (among 32 data sets with $n \geq 20$, r^2 ranged from 0.10-0.74). Furthermore, such plasticity may mean that King's (2000) prediction that the allometric coefficient relating female SVL and offspring number should equal three will be met only under conditions of resource abundance. This appears true in Lake Erie watersnakes where the allometric coefficient = 1.60 in the pre-round goby sample (95% CI = 0.62, 2.57) and 2.55 in the post-round goby sample (95% CI = 2.01, 3.01) (Fig. 1A) and in keelbacks where the allometric coefficient ranges from ca. 1.6 to 3.0 among years and is strongly correlated with prey abundance (Brown and Shine, 2007; fig. 2a).

Plasticity in life history itself may vary among snake populations. Experimental manipulation of resource availability in checkered gartersnakes (*Thamnophis marcianus*) had no effect on offspring number in a population from Arizona, USA but had a significant effect on a population from Texas, USA (Seigel and Ford, 2001). These two populations differ in the constancy of environmental conditions. The Texas population is subject to wide fluctuations in precipitation and hence, prey availability, whereas prey availability is relatively constant for the Arizona population. This observation suggests that differences in life history plasticity may be adaptive, although investi-

gation of alternative explanations is warranted (Seigel and Ford, 2001). Interestingly, although offspring size differed between Arizona and Texas populations of *T. marcianus*, offspring size was not affected by resource availability in either population. Thus, in both checkered gartersnakes and Lake Erie watersnakes, offspring size appears to be relatively buffered from environmental effects. Although quantitative genetic analyses of snake life history parameters are generally lacking, in keelbacks, offspring (egg) size has high heritability whereas offspring number does not (Brown and Shine 2006), a pattern consistent with the observation that offspring size is relatively invariant in response to environmental variation.

Results presented here suggest the possibility that resource availability may have contributed to population declines in Lake Erie watersnakes during the mid- to late-1900s. This period was associated with high nutrient loading, eutrophication, and aquatic food-web collapse (Ricciardi, 2001). Subsequent international efforts aimed at reducing nutrient loading reversed these trends (McGucken, 2000), although recent invasions by zebra mussels, quagga mussels, and round gobies have resulted in further food-web disruption (Stewart *et al.*, 1998; Ricciardi, 2001). While habitat loss and human-caused mortality are likely contributors to past watersnake population declines (Fazio and Szymanski, 1999), the possibility exists that a reduction in benthic fish biomass, resulting in reduced watersnake fecundity, was also a factor. Unfortunately, quantitative data on long-term temporal trends in benthic fish biomass are lacking.

A fundamental challenge facing ecologists, evolutionary biologists, and conservation biologists today is to understand the short- and long-term consequences of natural and anthropogenic environmental change. These may include both plastic and adaptive responses in life history, which in turn, contribute to population dynamics and likelihood of extinction. Long-term data sets, like that for the Lake Erie watersnake, are particularly valuable in this regard because they provide a baseline to which shorter-term data sets (as might be collected for species of conservation concern) can be compared. Furthermore, generalizations arising from long-term study (e.g., the suggestion here that offspring number shows a weaker relationship to female size under conditions of resource limitation) may have direct management implications; particularly for vulnerable populations such as those inhabiting islands where natural (Andren, 1982; Andren and Nilson, 1983) and artificial (this study) changes in prey availability may be especially pronounced.

RESUMO

Populações insulares da cobra-d'água do Lago Eire (*Nerodia sipedon insularum*) passaram por uma mudança ambiental dramática na forma de uma nova espécie de presa abundante, o gobiídeo redondo (*Neogobius melanostomus*). Os efeitos dessa mudança biótica nas características reprodutivas das cobras-d'água foram testadas pela comparação do tamanho da ninhada e da relação entre o tamanho da fêmea e o número de filhotes antes e depois da invasão pelo gobiídeo. O número de filhotes, mas não o tamanho dos mesmos, aumentou em consequência da mudança na dieta das cobras-d'água. Além disso, o tamanho da fêmea explicou uma maior proporção da variação no número de filhotes em seguida à invasão pelo gobiídeo (60% versus 25%). Estima-se que os efeitos combinados de um aumento no tamanho das fêmeas e no tamanho dos filhotes resultaram em um aumento de mais de 25% na fecundidade das cobras-d'água e devem estar estimulando o crescimento da população de cobras-d'água desde a invasão pelo gobiídeo. A rapidez com que ocorreu a mudança na dieta das cobras-d'água e a consequente mudança na fecundidade são consistentes com a hipótese de maximização da teoria de histórias de vida e sugere que a história de vida das cobras-d'água devia ser fortemente limitada pela disponibilidade de recursos antes da invasão pelo gobiídeo.

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