Journal of Herpetology, Vol. 27, No. 1, pp. 90–94, 1993

Microgeographic, Historical, and Size-correlated Variation in Water Snake Diet Composition

RICHARD B. KING, *Department of Biological Sciences, Northern Illinois University, Dekalb, Illinois 60115, USA.*

The diets of many species of snakes are poorly known because of the difficulty in observing feeding directly and the low frequency with which prey are recovered from live or preserved specimens. As a result, knowledge of prey composition is sketchy and patterns of variation in diet (geographic, ontogenetic) are virtually unknown for many species (reviewed by Mushinsky, 1987). However, for snakes which are locally abundant, an opportunity exists to obtain a much more complete understanding of feeding ecology (e.g., Mushinsky and Hebrard, 1977; Gregory, 1978, 1984; Kephart, 1982; Kephart and Arnold, 1982; Mushinsky et al., 1982).

In this note I report on the diet of the water snake *Nerodia sipedon*, which is locally abundant at island and mainland sites near Lake Erie. Two subspecies of water snakes occur in this area: the Lake Erie water snake, *N. s. insularum*, which is found on islands in western Lake Erie; and the northern water snake, *N. s. sipedon*, which is found at adjacent mainland sites (Conant and Clay, 1937, 1963). Here, I compare the diet of island and mainland snakes, and thus subspecies. This comparison is of interest from a management perspective because *N. s. insularum* is listed as endangered under the Ontario Endangered Species Act (McKeating and Bowman, 1977) and as a Category 2 species by the U.S. Fish and Wildlife Service (Anonymous, 1985). I also compare diet composition of island snakes between 1948 (using data from Hamilton, 1951) and the present. Finally, I analyze the relationship between snake size and prey size.

Prey were obtained from water snakes at three mainland and five island sites from 1989–1992. Mainland sites were Willow Point (Erie County, Ohio), Hillman Marsh (Essex County, Ontario), and St. Clair Marsh (Kent County, Ontario). Island sites were Middle Bass Island, North Bass Island (Ottawa County, Ohio), Pelee Island, Middle Island, and East Sister Island (Essex County, Ontario). The two most distant sites, St. Clair Marsh and Willow Point, are separated by 105 km. Islands range in size from 21–4091 ha and are 9.5–19.1 km from the nearest mainland point. Mainland sites consist of managed marshes that drain into Sandusky Bay (Willow Point), Lake Erie (Hillman Marsh), or Lake St. Clair (St. Clair Marsh). These sites have soil, clay, or silt substrates and much emergent vegetation. Island sites encompass both shorelines and marsh habitats. Island shorelines have a rock or gravel substrate and lack emergent vegetation. Island marsh habitats have sand or clay substrates and some emergent vegetation.

Prey were palpated from snakes or were regurgitated spontaneously while snakes were being handled. When possible, prey were identified to species. Intact and nearly intact prey were weighed to obtain wet mass and measured to obtain length (standard length for fish, snout–vent length for amphibians), maximum height, and maximum width. Incomplete prey (those which lacked more than small regions of the head, skin, or appendages) were excluded from analyses of prey size. Snakes were measured to obtain snout–vent length (SVL), weighed, classified by sex, and released. Preserved prey will be deposited at the Field Museum of Natural History, Chicago.

A total of 70 prey was recovered from 45 individual water snakes and consisted of fish (62 prey from 38 snakes) and amphibians (eight prey from seven snakes; Table 1). Usually a single prey item was recovered per snake but two prey were recovered from each of five snakes and four, eight, and ten prey were recovered from one snake each. In all cases in which multiple prey were recovered from a single snake and could be identified, prey were of the same species.

Species composition of water snake diets differed between island and mainland sites in that amphibians were recovered only from island snakes (Table 1). In addition, fish of the families Cottidae, Gadidae, and Percidae were recovered only from island snakes, whereas fish of the families Centrarchidae and Umbridae were recovered only from mainland snakes. Fish of the families Cyprinidae and Ictaluridae were recovered both from island and mainland snakes, but different species were found at island and mainland sites (Table 1).

Differences in species composition of island and mainland water snake diets may reflect differences in habitat, and hence prey availability, between sites. Marsh-dwelling species such as the central mudminnow (*Umbra limi*) may be unavailable to island snakes and lake-dwelling species such as the spottail shiner (*Notropis hudsonius*) and the mudpuppy (*Necturus maculosus*) may be unavailable to mainland snakes. One somewhat surprising result was that ranid frogs were not recovered from mainland snakes. Although these prey may be scarce at island sites (see below), they are relatively common at mainland sites (pers. obs.) and are utilized by *N. sipedon* elsewhere (Uhler et al., 1939; Lagler and Salyer, 1945; Raney and Roecker, 1947; Zelnick, 1966).

Finer-scale geographic variation in diet composition may also occur in the Lake Erie area (e.g., among island sites). For example, mudpuppies (*N. maculosus*) were recovered only from North Bass Island snakes

TABLE 1. Taxonomic distribution of prey from water snakes (*Nerodia sipedon*) at island and mainland sites near Lake Erie, 1989–1992.

Taxon	No. of prey (no. of snakes) Mainland	Islands
Fish		
Centrarchidae		
Lepomis cyanellus	1 (1)	
Cottidae		
Cottus bairdi		1 (1)
Cyprinidae		
Carassius auratus	14 (5)	
Cyprinella spiloptera	1 (1*)	
Notropis hudsonius		5 (2)
Notropis rubellus	2 (1)	
Notropis sp.		11 (2)
Unidentified Cyprinidae	1 (1*)	
Ictaluridae		
Ictalurus melas	1 (1)	
Ictalurus punctatus	1 (1)	
Ictalurus sp.	1 (1)	2 (2)
Noturus flavus		1 (1)
Gadidae		
Lota lota		2 (2)
Percidae		
Etheostoma flabellare		1 (1)
Percina caprodes		6 (5)
Percina sp.		2 (2)
Unidentified Percidae		2 (2)
Umbridae		
Umbra limi	1 (1)	
Unidentified fish	2 (2)	4 (4)
Amphibians		
Ambystomatidae		
Ambystoma sp.		2 (1)
Proteidae		
Necturus maculosus		6 (6)

* Recovered from the same snake.

(but see Hamilton, 1951) and burbot (*Lota lota*) were recovered only from Pelee Island snakes, but sample sizes are small. Fine scale geographic variation in diet resulting from variation in prey availability has been well-documented among local populations of garter snakes (*Thamnophis sirtalis, T. elegans*; Kephart, 1982; Gregory and Nelson, 1991), and among island and mainland populations of adders (*Vipera berus*; Forsman, 1991), black tiger snakes (*Notechis ater*; Schwaner, 1985; Shine, 1987), and *Elaphe quadrivirgata* (Hasegawa and Moriguchi, 1989). Furthermore, this variation in diet sometimes results in large differences in body size among snake populations (Schwaner, 1985; Shine, 1987; Hasegawa and Moriguchi, 1989; Forsman, 1991). Though modest differences in body size do exist among Lake Erie island and mainland water snake populations (R. King, 1989), further data

TABLE 2. Comparison of Lake Erie island water snake diet composition between 1948 (from Hamilton, 1951) and the present.

Taxon	1948	1989–1992
Fish		
Cyprinidae	X	X
Cottidae		
Cottus	X	X
Gadidae		
Lota		X
Ictaluridae[1]	X	X
Percidae		
Percina	X	X
Etheostoma		X
Amphibians		
Ambysomatidae		
Ambystoma		X
Bufonidae		
Bufo	X	X[2]
Proteidae		
Necturus	X	X
Ranidae		
Rana pipiens	X	
Rana clamitans	X	
Rana sp.	X	
Salamandridae		
Notophthalmus[3]	X	

[1] "Ameiurids" in Hamilton, 1951.
[2] From R. King, 1986.
[3] *Triturus* in Hamilton, 1951.

are needed to determine if these differences are related to diet.

Throughout its range in eastern North America, the diet of *N. sipedon* consists almost entirely of fish and amphibians though proportions of these prey types vary considerably (Drummond, 1983; R. King, 1986). In general, amphibian prey consist primarily of ranid frogs. Other anurans (e.g., *Bufo, Acris*) and salamanders (e.g., *Necturus, Eurycea, Notophthalmus*) are consumed only rarely (W. King, 1939; Uhler et al., 1939; Lagler and Salyer, 1945; Raney and Roecker, 1947; Brown, 1958; Zelnick, 1966). The predominance of *Necturus* among amphibians preyed upon by *N. sipedon* from Lake Erie presumably reflects the availability of these prey in lakes. *Necturus* also occurs in the diet of water snakes from Michigan lakes but not Michigan streams (Lagler and Salyer, 1945; Brown, 1958). Among fish, *N. sipedon* from Lake Erie and elsewhere commonly prey on sculpins (Cottidae), minnows (Cyprinidae), catfishes (Ictaluridae), and perches (Percidae), although species consumed vary from site to site (Uhler et al., 1939; Lagler and Salyer, 1945; Raney and Roecker, 1947; Brown, 1958; Zelnick, 1966; this study). Away from Lake Erie, suckers (family Catostomidae) are also important prey (W. King, 1939; Uhler et al., 1939; Lagler and Salyer, 1945; Raney and Roecker, 1947; Brown, 1958). This may also reflect differences in prey availability.

The presence of bottom-dwelling prey such as Ictaluridae, *Percina, Lota, Cottus,* and *Necturus* is consistent with the foraging behavior of *N. sipedon,* which devotes a large proportion of its aquatic foraging time

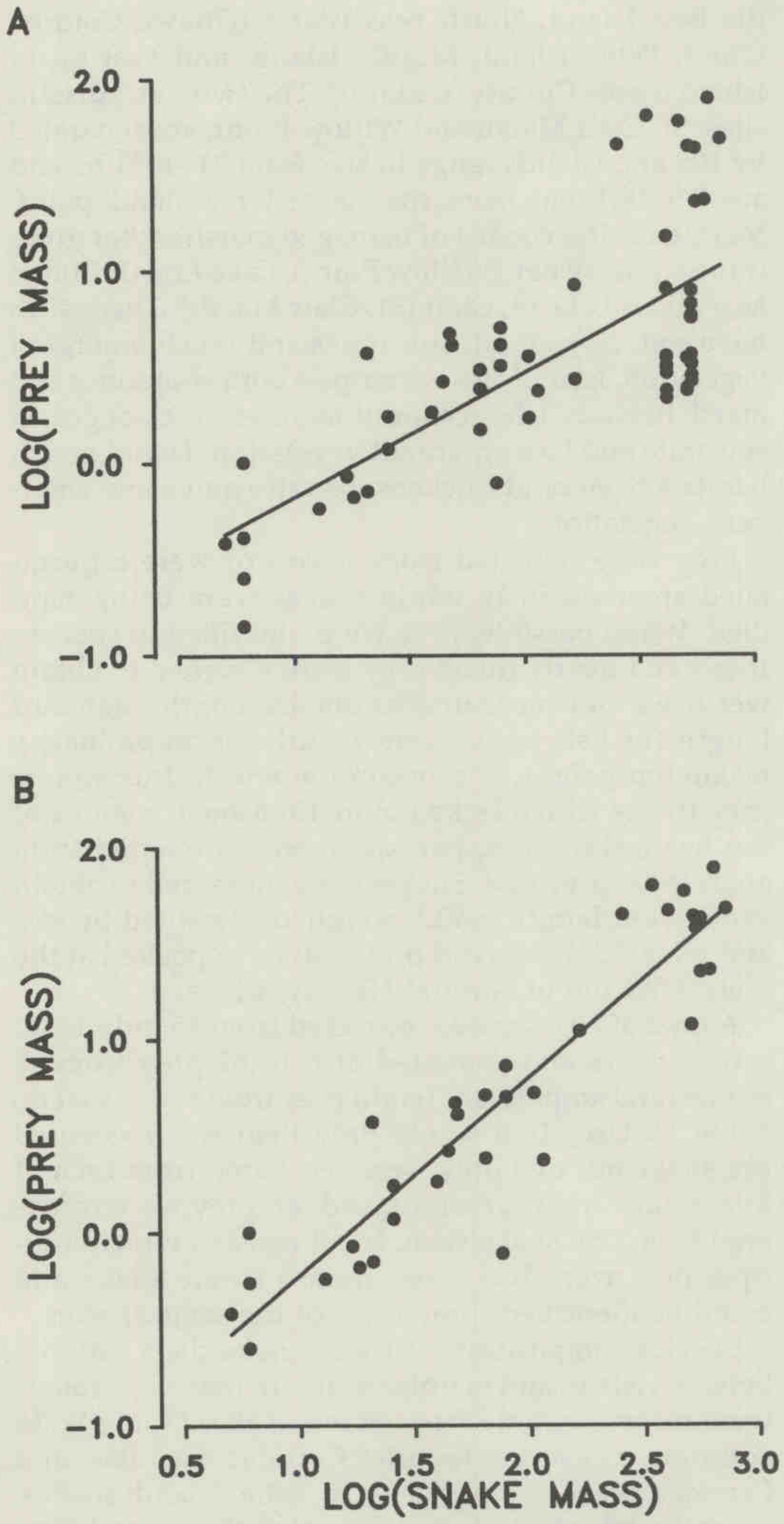

FIG. 1. (A) Relationship between log(snake mass) and log(individual prey mass) for the water snake *Nerodia sipedon.* Each point represents an individual prey and the line represents the least squares regression: log(prey mass) = 0.65 × log(snake mass) − 0.83, $R^2 = 0.51$, $P < 0.001$, N = 59 prey. (B) Relationship between log(snake mass) and log(total prey mass per snake). Each point represents an individual snake and the line represents the least squares regression: log(total prey mass per snake) = 1.02 × log(snake mass) − 1.24, $R^2 = 0.87$, $P < 0.001$, N = 35 snakes.

to investigating crevices and crawling on the substrate (Drummond, 1983).

Data on the past diet of island water snakes came from Hamilton (1951) who recovered prey items from 23 of 35 Pelee Island water snakes in the Cornell University collection. Diet composition differed significantly between 1948 and present samples (Table 2): whereas Hamilton (1951) recovered fish from 54% and amphibians from 52% of Pelee Island snakes containing prey in the 1948 sample, I recovered fish from 78% and amphibians from 22% of island snakes con-

TABLE 3. Summary statistics for measures of snake size and prey size. Linear measures are in mm, measures of mass are in g. Sample sizes vary because multiple prey were recovered from some snakes and because not all variables were measured for all snakes or prey.

	Mean ± SD	Minimum	Maximum	N
Snake SVL	579.12 ± 271.09	165	1000	42
Snake mass	218.79 ± 253.78	5	890	39
Prey length	65.50 ± 33.71	17	183	65
Prey height	17.14 ± 8.86	3	52	63
Prey width	10.02 ± 6.42	4	30	63
Prey mass	10.59 ± 17.68	0.14	77.00	66

taining prey in 1989–1992 (G = 4.008, df = 1, $P < 0.05$). Furthermore, of the amphibians recovered from island snakes, ranid frogs (*Rana pipiens, R. clamitans*) made up the majority of the 1948 sample (71% by mass) but were entirely absent from the 1989–1992 sample. Among fish prey, *Etheostoma* and *Lota* were recovered from the present sample but were absent from the 1948 sample.

Differences in the species composition of island water snake diet between 1948 and the present may reflect changes in prey availability. Although *Rana pipiens, R. clamitans,* and *R. catesbeiana* occur on some of the larger islands (Langlois, 1964; Kraus and Schuett, 1982; Weller and Oldham, 1988), they are present only at a few local sites (pers. obs.) and *R. pipiens* and *R. clamitans* are relatively rare: a seven-year compilation of reptile and amphibian records in Ontario includes only five records of *R. pipiens* and one record of *R. clamitans* (compared to 82 records of *R. catesbeiana*) for Pelee Island (Weller and Oldham, 1988; W. Weller and M. J. Oldham, pers. comm.). Although former population densities of these species are not known, pesticides and habitat degradation may have reduced populations from 1948 levels. Suitable amphibian breeding habitat on the islands is subject to runoff from adjacent agricultural areas. In addition, sand and gravel bars that separate several areas of potential amphibian breeding habitat from Lake Erie have breached, allowing entry of carp (*Cyprinus carpio*) which may interfere with amphibian reproduction by increasing turbidity. A recent decline in the number of cricket frogs (*Acris crepitans*) on Pelee Island is also evident (Oldham and Sutherland, 1986; Canadian Wildlife Service, 1990). Differences in diet composition between the 1948 sample and the present one may also reflect seasonal changes in prey availability although both samples span relatively long time periods (14 May–12 September in 1989–1992; April–July in 1948, Hamilton, 1951).

Snakes from which prey were recovered varied in size from newborns to large adults (Table 3). Prey size showed a similar range of variation (Table 3). For statistical analyses, measures of snake size (SVL, mass) and prey size (mass, length, height, width) were log transformed to meet assumptions of normality and homoscedasticity. All measures of prey size were significantly positively correlated with snake SVL and snake mass ($P < 0.05$), though only the analysis of snake mass and prey mass is reported here. Masses of individual prey ranged from <1% to 18% of water snake mass. Analysis of covariance revealed no difference in prey mass between male and female water snakes after removing the effect of snake body mass (F = 0.23, df = 1, $P = 0.64$) so the sexes were combined in determining the relationship between snake mass and prey mass. Individual prey mass was positively correlated with snake mass; heavier water snakes consumed heavier prey (Fig. 1A). This correlation was even stronger when masses of individual prey recovered from the same snake were summed (Fig. 1B). Larger snakes apparently excluded smaller prey; the smallest prey consumed by the largest snakes in this study were more than 10 times the mass of the smallest prey consumed by the smallest snakes (Fig. 1A). Prey species composition also differed between large and small snakes. For example, percid fish (N = 10) were only recovered from water snakes measuring less than 540 mm SVL whereas mudpuppies (*Necturus maculosus*) (N = 6) and burbot (*Lota lota*) (N = 2) were only recovered from snakes measuring more than 520 mm SVL. Because female water snakes exceed males in size (R. King, 1986), differences in diet between small and large snakes translate into differences between the sexes: mudpuppies and burbot were recovered only from female snakes. Such size related ontogenetic shifts and sex differences in diet occur in other species of water snakes as well (e.g., Mushinsky et al., 1982; Plummer and Goy, 1984).

Differences in size and species composition of prey consumed by large and small snakes may result from several mechanisms (Shine, 1991). Differences in prey size may arise because large and small snakes differ in their ability to capture, subdue, and swallow prey of different sizes. Differences in prey species composition may arise for the same reason if prey taxa differ in size. Differences in prey size and species composition may also arise if large and small snakes forage in different ways, in different places, or at different times. For example, small water snakes may be able to extract prey from smaller retreats (Shine, 1991). In contrast, larger water snakes may be better able to forage farther from shore and in deeper water (Pough, 1978). Further data on water snake foraging behavior and prey availability would aid in understanding differences in prey utilization between small and large (and male and female) water snakes.

Acknowledgments.—Methods were approved by the Ontario Ministry of Natural Resources Wildlife Branch and the Northern Illinois University Institutional Animal Care and Use Committee. Permits were provided by the U.S. Fish and Wildlife Service, U.S. Department of Agriculture, Ontario Ministry of Natural Resources, Essex Region Conservation Authority, Canadian Wildlife Service, and Ohio Department of Natural Resources. Logistical support was provided by the Ohio State University—F. T. Stone Laboratory. I especially thank the McTavish family for providing a home base on Pelee Island, Joan Bradley (Ohio State University, Mansfield) for identifying fish, and B. King and two reviewers for comments on the manuscript.

Literature Cited

Anonymous. 1985. Endangered and threatened wildlife and plants; review of vertebrate wildlife, notice of review. Federal Register 50(181):37958–37967.

Brown, E. E. 1958. Feeding habits of the northern water snake, *Natrix sipedon sipedon* Linneaus. Zoologica (N.Y.) 43:55–71.

Canadian Wildlife Service. 1990. COSEWIC review. Recovery: An Endangered Species Newsletter 2:4–5.

Conant, R., and W. Clay. 1937. A new subspecies of watersnake from the islands in Lake Erie. Occ. Pap. Univ. Michigan Mus. Zool. 346:1–9.

———, and ———. 1963. A reassessment of the taxonomic status of the Lake Erie water snake. Herpetologica 19:179–184.

Drummond, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. Behaviour 86:1–30.

Forsman, A. 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effect of prey size. J. Anim. Ecol. 60:253–267.

Gregory, P. T. 1978. Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island. Can. J. Zool. 56:1967–1974.

———. 1984. Habitat, diet, and composition of assemblages of garter snakes (*Thamnophis*) at eight sites on Vancouver Island. Can. J. Zool. 62:2013–2022.

———, and K. J. Nelson. 1991. Predation on fish and intersite variation in the diet of common garter snakes, *Thamnophis sirtalis*, on Vancouver Island. Can. J. Zool. 69:988–994.

Hamilton, W. J., Jr. 1951. Notes on the food and reproduction of the Pelee Island water snake, *Natrix sipedon insularum* Conant and Clay. Can. Field Natur. 65:64–65.

Hasegawa, M., and H. Moriguchi. 1989. Geographic variation in food habits, body size and life history traits of the snakes on the Izu Islands. Current Herpetology in East Asia 1989:414–432.

Kephart, D. G. 1982. Microgeographic variation in the diets of garter snakes. Oecologia (Berlin) 52: 287–291.

———, and S. J. Arnold. 1982. Garter snake diets in a fluctuating environment: a seven-year study. Ecology 63:1232–1236.

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

———. 1989. Body size variation among island and mainland snake populations. Herpetologica 45:84–88.

King, W. 1939. A survey of the herpetology of the Great Smoky Mountains National Park. Amer. Midl. Natur. 21:531–582.

Kraus, F., and G. Schuett. 1982. A herpetofaunal survey of the coastal zone of northwest Ohio. Kirtlandia 36:21–54.

Lagler, K. F., and J. C. Salyer II. 1945. Food and habits of the common watersnake, *Natrix s. sipedon*, in Michigan. Pap. Michigan Acad. Sci., Arts and Letters 31:169–180.

Langlois, T. 1964. Amphibians and reptiles of the Erie islands. Ohio J. Sci. 64:11–25.

McKeating, G., and I. Bowman. 1977. Endangered species issue. Ontario Fish and Wildlife Review 16:1–24.

Mushinsky, H. R. 1987. Foraging ecology. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), Snakes: Ecology and Evolutionary Biology, pp. 302–334. Macmillan Publ. Co., New York.

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

———, ———, and D. S. Vodopich. 1982. Ontogeny of water snake foraging ecology. Ecology 63:1624–1629.

Oldham, M. J., and D. A. Sutherland. 1986. 1984 Ontario herpetofaunal summary. Essex Region Conservation Authority, Essex, Ontario.

Plummer, M. V., and J. M. Goy. 1984. Ontogenetic dietary shift of water snakes (*Nerodia rhombifera*) in a fish hatchery. Copeia 1984:550–552.

Pough, F. H. 1978. Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): physiological correlates and ecological consequences. Copeia 1978:69–75.

Raney, E. C., and R. M. Roecker. 1947. Food and growth of two species of watersnakes from New York. Copeia 1947:171–174.

Schwaner, T. D. 1985. Population structure of black tiger snakes, *Notechis ater niger*, on offshore islands of South Australia. *In* G. Grigg, R. Shine, and H. Ehmann (eds.), Biology of Australasian Frogs and Reptiles, pp. 35–46. Royal Zool. Soc. New South Wales.

Shine, R. 1987. Ecological comparisons of island and mainland populations of Australian tigersnakes (*Notechis: Elapidae*). Herpetologica 43:233–240.

———. 1991. Why do larger snakes eat larger prey items? Funct. Ecol. 5:493–502.

Uhler, F. M., C. Cottam, and T. E. Clarke. 1939. Food of snakes of the George Washington National Forest, Virginia. Trans. 4th N. Amer. Wildlife Conf. 1939:605–622.

Weller, W. F., and M. J. Oldham (eds.). 1988. Ontario Herpetofaunal Summary 1986. Ontario Field Herpetologists, Cambridge, Ontario.

Zelnick, G. E. 1966. Midsummer feeding habits of the midland water snake. Southwest. Natur. 11: 311–312.

Accepted: 27 October 1992.