

BODY SIZE VARIATION AMONG ISLAND AND MAINLAND SNAKE POPULATIONS

RICHARD B. KING¹

*Department of Biological Sciences, University of Cincinnati,
Cincinnati, OH 45221, USA*

ABSTRACT: Body size of adult garter snakes (*Thamnophis sirtalis*) and adult water snakes (*Nerodia sipedon*) varied significantly among eight island and three mainland sites in the Lake Erie area. Among the six sites at which both species were sampled, mean adult snout-vent length of garter snakes was positively correlated with that of water snakes for females but not for males. Explanations for geographic variation in body size and for parallel variation in body size between species include differences in individual growth rate and differences in population age-structure among sites.

Key words: *Thamnophis sirtalis*; *Nerodia sipedon*; Island populations; Body size

BODY size may vary geographically because of differences in individual growth rate or differences in population age-structure among sites (Andrews, 1982). These differences may arise from geographic variation in climate, food resources, interspecific competition, intraspecific competition, predation intensity, or other sources of mortality (Dunham et al., 1978). Geographic variation in body size has been documented in a number of snake taxa (e.g., Case, 1978; Fitch, 1981; Parker and Plummer, 1987; Plummer, 1987; Schwaner, 1985; Shine, 1987), but the reasons for this variation are often obscure. Case (1978) suggested that island snakes are typically smaller than conspecific or congeneric mainland snakes because of reduced food resources. The impact of varying food resources on the body size of black snakes (*Notechis ater*) in island populations was clearly demonstrated (Schwaner, 1985). Differences in age-structure have been invoked less frequently to explain geographic variation in body size. Here, I describe patterns of body size variation in garter snakes (*Thamnophis sirtalis*) and water snakes (*Nerodia sipedon*) among mainland and island populations in the Lake Erie area and discuss possible explanations for this variation.

MATERIALS AND METHODS

Data on garter snakes and water snakes were collected from 1980-1985 in conjunction with an investigation of color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum* (King, 1985, 1986, 1987). Garter snakes were studied on seven islands (Kellys, Middle, Pelee, North Bass, Middle Bass, East Sister, West Sister) and at two mainland sites (Little Portage Wildlife Area, East Harbor State Park). Water snakes were studied on six islands (Kellys, Middle, Pelee, North Bass, Middle Bass, Johnsons) and at two mainland sites (Little Portage Wildlife Area, Willow Point Wildlife Area). Localities are shown in King (1988:Fig. 1). Snakes were captured by hand, probed to determine sex, measured to the nearest 1 cm to obtain snout-vent length (SVL), individually marked by clipping ventral scales, and released at the point of capture (details in King, 1985, 1986, 1988). Snakes were classified as juveniles or adults based on size (King, 1985, 1986, 1988). For garter snakes, males >35 cm SVL and females >45 cm SVL were classified as adults. For water snakes, males >42 cm SVL and females >58 cm SVL were classified as adults.

Adult SVL was compared among sites and between sexes by analysis of variance (ANOVA) after testing for normality and equality of variances using SPSS (Nie et al., 1975). Water snakes and garter snakes

¹ PRESENT ADDRESS: Biology Department, Indiana University, Bloomington, IN 47405, USA.

TABLE 1.—Two-way analysis of variance of SVL by sex and site for *T. sirtalis*. Kellys Island was excluded from this analysis, because only a single adult male was captured there.

Source	Sum of squares	df	Mean square	F	P
Main effects	30,028.594	8	3753.574	73.433	0.001
Sex	7127.596	1	7127.596	139.441	0.001
Site	15,138.886	7	2162.698	42.310	0.001
Sex × site	471.024	7	67.289	1.316	0.241
Explained	30,499.618	15	2033.308	39.779	0.001
Residual	22,030.802	431	51.116		
Total	52,530.421	446	117.781		

were analyzed separately. A posteriori Student-Newman-Keuls (SNK) tests were used to identify groups of sites homogeneous in SVL; SNK tests were based on residual mean squares from one-way ANOVA's calculated separately for each sex and species. Pearson correlation coefficients were subjected to one-tailed significance tests to determine if mean adult SVL was positively correlated between sexes and between species. Between species comparisons were restricted to the six sites where both species were sampled. For snakes captured more than once, only data from initial capture were analyzed. A significance level of $\alpha = 0.05$ was used in all analyses.

RESULTS

Sex and site both explained significant amounts of variation in adult garter snake size (Table 1). Among adult garter snakes of both sexes, mean SVL was smallest at East Harbor. Mean SVL was largest on Middle Island in adult females and on West

Sister Island in adult males. Mean SVL differed by as much as 12 cm among sites in adult males and 14 cm in adult females (Table 2). Among the nine sites, mean SVL of adult male garter snakes was positively correlated with that of adult females ($r = 0.60$, $n = 9$, $P < 0.05$). A SNK test revealed two groups of sites for which SVL was homogeneous in each sex (Table 2).

As in garter snakes, sex and site both explained significant amounts of variation in adult water snake size (Table 3). Among adult water snakes of both sexes, mean SVL was greatest on Middle Island and least at Little Portage Wildlife Area. Mean SVL differed by as much as 13 cm among sites in adult males and 11 cm in adult females (Table 4). Among the eight sites, mean SVL of adult male water snakes was positively correlated with that of adult females ($r = 0.94$, $n = 8$, $P < 0.0005$). A SNK test revealed two groups of sites for which SVL was homogeneous in adult males (Table 4). Adult females did differ in SVL among sites based on a one-way ANOVA ($F = 3.181$, $df = 7$, $P = 0.03$),

TABLE 2.—Mean SVL (cm) of adult male and female *T. sirtalis* from nine sites in the Lake Erie area. Values followed by different letters differ significantly in SVL (Student-Newman-Keuls test, $\alpha = 0.05$). Island areas are indicated in parentheses.

Site	Sex					
	Female			Male		
	SVL	n	Variance	SVL	n	Variance
East Harbor State Park	55.3 a	41	40.2	44.5 a	33	37.6
Middle Bass Island (300 ha)	55.7 a	40	32.9	46.1 a	12	17.7
North Bass Island (282 ha)	56.0 a	28	49.0	45.6 a	16	10.4
Little Portage	56.4 a	19	45.9	49.3 a,b	4	54.3
Pelee Island (4091 ha)	58.2 a	57	49.9	52.2 b	24	18.5
East Sister Island (26 ha)	66.7 a,b	3	26.3	49.0 a,b	2	338.0
West Sister Island (28 ha)	68.3 b	39	50.6	57.0 b	6	94.0
Kellys Island (1169 ha)	68.5 b	6	228.3	46.0	1	
Middle Island (21 ha)	69.3 b	112	80.2	56.4 b	11	36.5

TABLE 3.—Two-way analysis of variance of SVL by sex and site for *N. sipedon*.

Source	Sum of squares	df	Mean square	F	P
Main effects	69,662.574	8	8707.822	102.845	0.001
Sex	60,741.644	1	60,741.644	717.396	0.001
Site	6597.750	7	942.535	11.132	0.001
Sex × site	550.953	7	78.708	0.930	0.483
Explained	70,213.527	15	4680.902	55.284	0.001
Residual	8845.347	695	84.670		
Total	129,058.874	710	181.773		

but a SNK test showed all sites to be a single homogeneous group.

Both garter snakes and water snakes were sampled at six sites (Little Portage Wildlife Area, Middle Bass Island, North Bass Island, Pelee Island, Middle Island, Kellys Island). Among these six sites, mean adult SVL of female garter snakes was positively correlated with that of female water snakes ($r = 0.92$, $n = 6$, $P < 0.005$) (Fig. 1). Mean adult SVL of male garter snakes was not correlated with that of male water snakes ($r = 0.26$, $n = 6$, $0.20 > P > 0.10$) (Fig. 1). Males of both species were largest on Middle Island, but sizes did not correspond at other sites.

DISCUSSION

Variation in body size of garter snakes and water snakes among sites in the Lake Erie area is unusual in that it occurs over a small geographic area and varies in parallel between species, at least in females. Though samples from some sites are small, variation in body size does not appear to be solely an artifact of sample size: mean SVL varies by >7 cm among sites with sample sizes of 20 or more. Nor does vari-

ation in body size appear to result from differences in sampling procedures among sites. Seasonal timing of sampling could bias mean SVL if snakes of different sizes have different seasonal activity patterns. However, capture methods were the same at all sites and sites were visited repeatedly throughout the active season of *T. sirtalis* and *N. sipedon*.

In contrast to the suggestion of Case (1978), body size in island populations is not smaller than that observed in mainland populations included in this study. SNK tests indicate that six of the seven groups of sites homogeneous for SVL include both mainland and island sites (Tables 2 and 4). Furthermore, body sizes of snakes in the Lake Erie area appear to be as large as (garter snakes) or larger than (water snakes) those observed in mainland populations elsewhere. Among sites in Michigan, Kansas, Ontario, Washington, Indiana, and Oregon, mean SVL of *Thamnophis sirtalis* ranges from 45.3–51.9 cm for males and 51.5–63.6 cm for females (Carpenter, 1952; Fitch, 1981; Gibson, 1978; Hebard, 1950; Minton, 1972; Stewart, 1968). In the Lake Erie area, males average 48.7 cm (range

TABLE 4.—Mean SVL (cm) of adult male and female *N. sipedon* from eight sites in the Lake Erie area. Values followed by different letters differ significantly in SVL (Student-Newman-Keuls test, $\alpha = 0.05$). Island areas are indicated in parentheses.

Site	Sex					
	Female			Male		
	SVL	n	Variance	SVL	n	Variance
Little Portage	74.3 a	7	110.6	55.4 a	7	22.3
Middle Bass Island (300 ha)	78.4 a	50	123.3	60.7 a,b	51	77.5
Willow Point	79.5 a	15	105.3	58.4 a,b	11	45.7
North Bass Island (282 ha)	79.5 a	91	82.1	61.4 a,b	133	73.7
Pelee Island (4091 ha)	80.5 a	63	129.7	58.8 a,b	103	78.5
Kellys Island (1169 ha)	84.5 a	53	98.8	67.7 b	53	63.2
Johnsons Island (27 ha)	85.7 a	21	79.2	67.7 b	26	21.6
Middle Island (21 ha)	85.7 a	13	111.2	68.9 b	14	88.2

of means among sites = 44.5–56.4 cm) and females average 62.3 cm (range of means among sites = 55.3–69.3 cm). At sites in Kansas and Michigan, mean SVL of *Nerodia sipedon* is 46.6 and 52.5 cm in males and 69.0 and 67.7 cm in females (Beatson, 1976: estimated from Fig. 1; Feaver, 1977). In the Lake Erie area, males average 62.0 cm overall (range of means among sites = 55.4–68.9 cm) and females average 81.0 cm overall (range of means among sites = 74.3–85.7 cm).

Does variation in adult body size of garter snakes and water snakes among sites in the Lake Erie area result from differences in growth rate? Growth rate may vary among sites because of differences in climate, food resources, intraspecific competition, or interspecific competition. Macro-climate is likely to be similar among sites, because distances are small (<20 km) and all sites are within the thermal shadow of Lake Erie. However, micro-climate may vary due to differences in exposure or vegetation. In the Lake Erie area, water snakes and garter snakes utilize different prey. Water snakes feed almost exclusively on aquatic prey (mostly fish: King, 1986). Garter snakes appear to feed more on soft-bodied terrestrial prey (fish were never found among their stomach contents, and unlike water snakes, garter snakes were never seen swimming offshore). This difference in diet suggests that competition for food between garter snakes and water snakes is likely negligible. Furthermore, because of these dietary differences, variation in food resources or in intraspecific competition among sites is not expected to result in the pattern of parallel variation between species seen in this study.

Does variation in adult body size of garter snakes and water snakes among sites in the Lake Erie area reflect variation in age-structure? Differences in age-structure among sites may result from variation in predator intensity or in other causes of mortality. Sites do differ in potential predator species present (e.g., herons, gulls, foxes, racoons, domestic cats and dogs: personal observation), and this may result in differences in predation intensity. Sites may also differ in winter mortality due to dif-

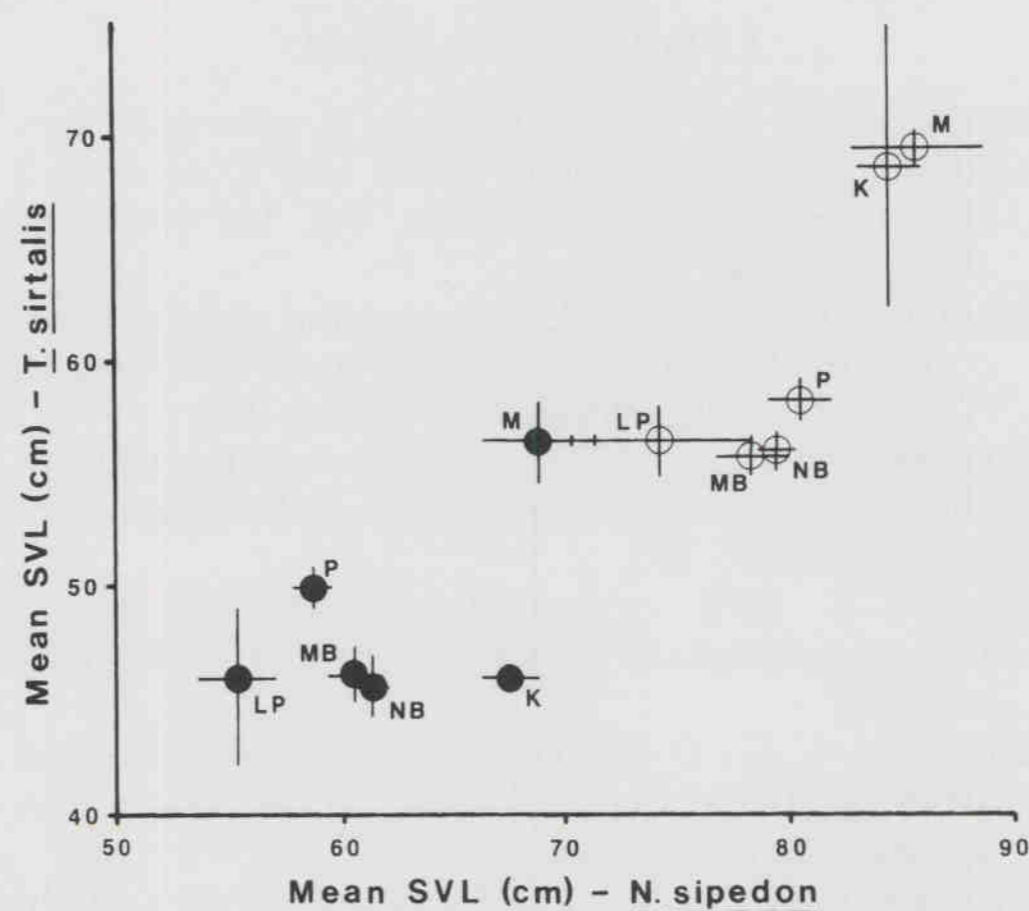


FIG. 1.—Correspondence in mean SVL (cm) between *T. sirtalis* and *N. sipedon* among sites. There is a significant positive correlation between species for adult females (open circles) but not for adult males (closed circles). Bars represent 1 SE on either side of the mean. Sites are identified by letters: LP = Little Portage, MB = Middle Bass, NB = North Bass, P = Pelee, K = Kellys, M = Middle.

ferences in quality of hibernation sites. At many sites, especially small, low-lying islands (which rise as little as 2 m above lake level), piles of loose limestone and dolomite along the shoreline appear to provide the only hibernation sites available to either species (personal observation). These rock piles may be overturned by winter and spring storms resulting in periodically high winter mortality in snakes hibernating there. Populations recovering from such declines are expected to consist of a greater proportion of younger and thus smaller snakes than populations which have gone for some time without suffering mortality from this source. Parallel geographic variation in body size between species may result from similarities between species and differences among sites in the likelihood of and time since such population declines.

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