Spatial Ecology of the Concho Water Snake (Nerodia harteri paucimaculata) in a Large Lake System

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ABSTRACT.—The distribution, movements, activity range, and habitat use of the Concho water snake, *Nerodia harteri paucimaculata*, were studied by mark-recapture and radio telemetry in a large lake system, in central Texas, USA. Concho water snake emigration and distribution were largely driven by alteration of habitat availability caused by fluctuating water levels. Habitat characteristics associated with the presence of snakes at the study area were turbid water, minimal wave action, a gentle shoreline gradient, a silt substrate, and a rocky shoreline. Males and gravid females were equally vagile, and the likelihood of a snake undertaking an emigrational movement was independent of age and/or reproductive condition. However, males had significantly more movement days than gravid females. Radio-tagged males had detectable movements on 64% of monitored days, compared to 43% of monitored days for gravid females. Mean activity range length was 278 m for males, 219 m for gravid females, and 210 m for juveniles. Concho water snakes generally selected retreat sites within 3 m of water, although gravid females selected sites as far as 15 m from water. As a management procedure for lake populations, we advocate increasing the vertical distribution of rocky shoreline.

Animal spatial patterns often reflect the availability and distribution of resources relative to the physiological requirements of the organism. In snake populations, spatial patterns are often population-specific and motivated by various factors. For example, differential resource requirements among population subunits may introduce considerable intraspecific variation in spatial patterns and habitat use (Gregory et al., 1987; Reinert, 1993). Spatial patterns may also vary temporally due to seasonal factors such as reproductive activity and migration among habitat types. Therefore, analyses of snake spatial patterns should consider the age, sex, and reproductive condition of each individual studied relative to observed seasonal variation (Gregory et al., 1987; Reinert, 1992; Secor, 1992, 1994; Charland and Gregory, 1995).

Little is known about the spatial ecology of snakes occurring in temporally volatile habitats. Houston and Shine (1994) reported high dispersal rates for filesnakes (*Acrochordus arafurae*) among billabongs, attributable to fluctuating water levels. They also cite extensive wet season movements for water pythons (*Liasis fuscus*) (Madsen and Shine, unpubl. data). The above studies illustrate the importance of environmental variables on snake spatial ecology in natural systems. The present study deals with a population of Concho water snakes in an artificial environment (a reservoir), subject to controlled water releases, thereby creating a temporally volatile environment.

Nerodia harteri paucimaculata is endemic to the Concho and Colorado Rivers of central Texas, and some of their tributaries (Scott et al., 1989). The Concho water snake is currently listed as endangered by the state of Texas and threatened by the U.S. Fish and Wildlife Service, a status conferred largely as a result of its limited distribution and the concurrent threat of habitat degradation and destruction. The threat of habitat destruction has been largely due to reservoir construction, resulting in habitat loss from decreased stream flows, sedimentation, and vegetation encroachment (Scott et al., 1989). Although populations may persist in degraded habitat, densities are greatly reduced (pers. obs.), which may increase the likelihood of local extirpations. With the impending construction of Ivie Reservoir and the subsequent inundation of a significant portion of Concho water snake habitat, assessment of the ecological attributes of lake populations became imperative. Of special interest was a population persisting in E. V. Spence Reservoir, constructed in 1969. Data obtained from the Spence Reservoir population may be applied to the future management of the Ivie Reservoir population.

MATERIALS AND METHODS

Study Area.—Field work took place at E. V. Spence Reservoir (hereafter called Spence). At the time of study, this was a 24-yr old reservoir of 14,950 ha surface area at maximum pool level, located in Coke County, Texas, USA (Fig. 1). The

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FIG. 1. Concho water snake distribution at E. V. Spence Reservoir for 1987–1991. The numbered well sites depicted contained Concho water snakes when sampled during 1990–91. Well sites which did not contain snakes at the time of sampling are not shown.

shoreline was largely devoid of vegetation (occasionally salt cedar [*Tamarix* sp.] was present), and consisted of a silt substrate, with occasional rocky stretches. Spence was a dynamic system constantly fluctuating in elevation (Fig. 2), causing spatial and temporal variation in habitat availability.

Two primary study sites were selected at Spence. Pump Station was located on the northwestern shoreline, facing the main body of the



FIG. 2. Maximum and minimum elevation (m) for E. V. Spence Reservoir during 1970–mid 1992.

lake, and Pecan Creek was located in the upper reaches of the lake, in a more sheltered environment (Fig. 1). The two sites were disjunct, and no evidence of population exchange was found (marked snakes from one site were not recaptured at the other site). Differences in location and orientation resulted in Pump Station receiving more intensive wave action from winds coming off the main body of the lake than Pecan Creek. Another important site difference was the abrupt shoreline gradient at Pump Station, compared to the more gradual shoreline of Pecan Creek. Both sites were characterized by rocky shorelines devoid of vegetation; however, when the lake elevation rose in 1992, the new shoreline at Pecan Creek entered a growth of salt cedar with less exposed rock.

In the upper northwestern reaches of Spence, a series of oil well sites (hereafter called well sites) existed either as islands or part of the shoreline. These well sites were conically shaped with rock-strewn slopes which ensured a constant rocky shoreline, regardless of water level. Well sites were only sampled in 1990, 1991, and briefly in 1992. General Procedures.—Snakes were captured by hand or in funnel traps (Fitch, 1987), placed along the shoreline. Nerodia h. paucimaculata were marked using radio frequency (RF) tags (Camper and Dixon, 1988). Upon capture, the following data were taken: snout-vent length (SVL; ± 1 mm), tail length (± 1 mm), mass (± 0.1 g), sex, reproductive condition, location, and habitat type. Habitat was visually characterized as shoreline, a creek/cove, or a well site.

Snake Distribution and Habitat Use.-Data on the distribution of Concho water snakes at Spence were collected in 1987 (16 sampling days) and 1988 (15 sampling days) through random shoreline searches conducted by a field crew of the Colorado River Municipal Water District (CRMWD). Shoreline containing rock was searched randomly and trapped over multiple days during 1990 (42 sampling days), 1991 (98 sampling days), and 1992 (25 sampling days) to investigate changes in the distribution of snakes in the lake basin. The results of these surveys were compared with those of 1987 and 1988, and general patterns of habitat use were discerned from these data. Habitat loss was not measured, but was noted when rocky shoreline was inundated or replaced by silt as a result of an elevation change. Additional data on habitat use obtained from telemetrically monitored snakes were compared with capture data to assess potential sampling bias due to differential catchability among habitats (see Whiting et al., 1996).

Movements.—Movement data were obtained from two shoreline localities (Pecan Creek and Pump Station) and several well sites (Fig. 1) using radio telemetry and shoreline trapping. Radio transmitters (Wildlife Materials Inc., Carbondale, Illinois) weighed ca. 3.5 or 5 g, and never exceeded 5% of a snake's body mass. Ten snakes, five of each sex, were surgically implanted with radio transmitters (Shine, 1979) and released within 24 h or surgery. Snakes were subsequently tracked using a Telonics TR-2 portable receiver and accompanying threeelement Yagi antenna. Transmitter life was approximately 180 d. Due to the constraints of body size, only adult snakes were fitted with radio transmitters. Snakes were checked once or twice daily, although less frequently in 1990. No snakes were tracked beyond a single season. Movement data were quantified for both rate (mean distance moved/day including nonmovement days) and magnitude (mean distance moved/day excluding nonmovement days).

Activity Range.—Activity range data were collected by both mark-recapture and radio telemetry. Study areas were demarcated at 10-m intervals to facilitate individual location. Swimming snakes detected by telemetry were generally underwater and difficult to locate, they were therefore excluded from this analysis. Prior to data analysis, snakes were placed in the following life history categories based on size at maturity and/or reproductive condition (Greene, 1993): (1) juveniles (males <380 mm SVL; females <460 mm SVL); (2) adult males; (3) nongravid adult females; and, (4) gravid females.

The exclusion of open water movements as a component of activity range prevented the analysis of activity range as a convex polygon (Jennrich and Turner, 1969), or as a harmonic mean (Dixon and Chapman, 1980). Instead, activity range was evaluated as a measure of linear shoreline, and the mean activity range length was computed for between three and 10 captures, for each life-history category. Activity range length was plotted as a function of the number of captures upon which they were based and the point of inflection taken to be the most representative activity range length. This allowed determination of the optimum number of captures for activity range measurement (Tinkle et al., 1962). An insufficient number of captures of nongravid adult females precluded such an analysis for this group.

The distance from water (m) was measured each time a telemetered snake was located. This was done only for telemetrically monitored snakes to avoid a sampling bias in favor of snakes found near the waters' edge.

Statistical Analysis.—Data were analyzed using STATISTIX (Analytical Software, 1990) and the Statistical Analysis System software program (SAS, 1989). Statistical procedures follow Sokal and Rohlf (1981). Data did not meet the assumptions of parametric statistics, therefore only nonparametric Mann-Whitney tests were used. In cases where the Mann-Whitney tests was used for samples >20, the normal approximation statistic with continuity correction (t_s) was applied. Chi-square tests were used for categorical data. All means are reported ± 1 SE. Differences were considered significant at the 0.05 alpha level.

RESULTS

Snake Distribution and Habitat Use.—Concho water snake distribution at Spence was dynamic over the five year period (Fig. 1), corresponding to fluctuations in lake surface elevation (Fig. 2). The presence of rocky shoreline was critical for Concho water snakes, and elevation changes of less than a meter were sometimes sufficient to alter habitat availability. Lake fluctuations resulted in loss of habitat in some areas (e.g., Rough Creek, Yellow Wolf Creek), and "creation" of habitat in others (e.g., parts of Cedar Cove and Pump Station site; Figs. 1 and 3). Re-



FIG. 3. (A) Pump Station at E. V. Spence Reservoir during 1990, a steep drop off prevented access by Concho water snakes; (B) Pump Station at Spence during 1992, after an increase in lake elevation. The habitat in the foreground was then available to Concho water snakes.

duced lake surface elevations at Spence continued throughout 1990–1991 because of low rainfall and controlled releases to reduce chloride levels.

During 1990–1991, no snakes were found at seven sites that contained snakes in 1987–1988 (Fig. 1). For the same period, only one new shoreline locality (Pecan Creek; well sites excluded), was discovered. Of seven well sites trapped, four contained Concho water snakes at the time of sampling, although relatively few snakes were found at each site (1–3 individuals at any one time). The Pump Station and Pecan Creek populations had the greatest concentra-

TABLE 1. Concho water snake capture statistics by habitat. Combined captures include both hand and trap caught snakes. Percent capture success includes only trap caught individuals, and negates the bias of differential sampling. Numbers in parentheses are numbers of individuals.

Habitat type	Combined captures	Trap nights	Trap captures	% capture success
Shoreline	646 (236)	4879 (90)	323 (90)	6.6
Creeks/coves	62 (37)	1034 (24)	46 (24)	3.2
Well sites	48 (26)	1637 (14)	33 (14)	2.8

tion of snakes (see Whiting et al., 1996). These sites also had the most rock of any site (except the dam, which contained no Concho water snakes during 1990-91). Pump Station contained snakes during all years surveyed. This site also appeared to be a stable habitat, as a continuous rocky gradient existed in most places, providing rock cover regardless of lake surface elevation. During late 1991 and the first half of 1992, heavy rainfall caused a dramatic rise in lake surface elevation (Figs. 2, 3), and habitat at the two primary sites (Pump Station and Pecan Creek) was impacted. At Pecan Creek, the lake edge extended into salt cedar (Tamarix) growth, with a corresponding reduction of retreat sites (see Movements). At Pump Station, a section of low elevation habitat in the form of a peninsula became submerged. This peninsula was strewn with large siltstone boulders which were often used by snakes. A telemetrically monitored female hibernated under one such siltstone boulder $(1.1 \times 1.4 \text{ m})$, 0.9 m from water during the winter of 1990.

Snakes consistently used rock structures for

shelter objects including single rocks, rock conglomerates, and crevasses between shelf rock. Telemetered snakes were always associated with rocky shoreline or nearby artificial cover. At Pump Station, two telemetrically monitored gravid females used the ramp of a large metal barge as a refuge. This barge was used on 43% (N = 64) of location days for one gravid female, and 48% (N = 47) of location days for the other. Individuals of both sexes occasionally used the bases of dead trees, in conjunction with small rock conglomerates, as shoreline refugia. Three broad habitat categories containing rock were identified: shoreline, creeks/coves, and well sites (Table 1). The highest capture success occurred along shoreline (Table 1). More individual snakes were caught along shoreline (χ^2_2 = 79.93, P < 0.0001) than the other two habitat categories.

Movements.—Of the 10 snakes implanted with radios, two were lost to predation, the first after 26 d, the second after 14 d. A third snake was lost after three days, but transmitter failure was suspected. Teeth marks on the two recovered transmitters suggested predation by a mammalian carnivore (skunk, raccoon, or coyote).

Data are presented only for snakes with a minimum of 10 observation days (N = 8; Table 2). Movement rates were analyzed from a total of 307 observations (one observation/day). Of 307 observations, 48 were for a single nongravid female, 99 for four males, and 160 for three gravid females (Table 2). For all 307 observations, the mean distance moved/day was 30.9 m (SE = 3.5, range = 0-458.9). Only adult male and gravid female movements were compared statistically. Adult male and gravid female Concho water snakes did not move significantly different daily distances (one-tailed Mann-Whitney

TABLE 2. Summary data on movements (m) obtained from nine telemetered Concho water snakes at E.V. Spence Reservoir during 1990–91. Movement rate is defined as the mean distance moved/day, including non-movement days; movement magnitude is defined as the average distance moved/day, excluding nonmovements. Means \pm 1 SE (in parentheses) are reported.

ID.	Sex	Movement rate	Movement magnitude	Longest movement	Duration tracked	# movement days/# days located	# move- ments >50 m
1750	ð	21.2 (5.1)	29.6 (6.9)	156.0	67 days	29/50	4
0858	ð	128.1 (41.2)	153.7 (45.3)	458.9	30 days	11/15	8
1107	ð	57.3 (11.2)	65.9 (11.8)	164.0	30 days	20/25	8
1383	ð	14.9 (6.0)	20.4 (7.5)	72.0	26 days	7/14	3
0963	Ŷ	13.3 (3.9)	31.1 (8.1)	118.5	73 days	23/64	7
1161	Ŷ	30.9 (10.9)	22.9 (8.9)	373.0	63 days	29/54	5
1594*	Ŷ	31.3 (6.9)	42.4 (8.8)	229.0	156 days	29/51	9
0704	Ŷ	31.3 (8.1)	67.0 (13.7)	243.0	149 days	19/47	12
1238**	Ŷ			390.0	14 days		

* Nongravid female.

** Lost to predation. Long movement was between habitats.

TABLE 3. Mean activity range (m) of adult male, gravid female, and juvenile Concho water snakes at E. V. Spence Reservoir, computed for a given number of captures. Numbers in parentheses are numbers of individuals; numbers below are 1 SE.

	Number of captures							
	3	4	5	6	7	8	9	10
Adult males	149 (18)	185 (11)	205 (10)	240 (8)	278 (7)	265 (6)	283 (6)	287 (6)
	38.2	64.9	69.4	83.8	90.8	120	113.4	112.1
Gravid females	91 (12)	93 (10)	126 (9)	203 (8)	219 (7)	218 (5)	189 (4)	189 (4)
	27.2	28.3	42.6	53.4	61.3	72.3	84.7	84.7
Juveniles	96 (24)	131 (10)	143 (9)	160 (7)	210 (4)	215 (4)	172 (3)	197 (2)
	15.6	32.9	34.8	42.2	72.5	75.5	87.8	146

 $U_1 = 4$, $U_2 = 8$, P = 0.31). The single nongravid female moved similar daily distances to adult males (Table 2). For all observations (99), males moved a mean distance/day of 41.6 m (SE = 7.1, range = 0-458.9); gravid females (160 observations) moved a mean daily distance of 24.1 m (SE = 4.5, range = 0-373); and the single nongravid female (48 observations) moved a mean daily distance of 31.3 m (SE = 6.9, range = 0–229). After taking the average for each individual, Concho water snakes (sexes and reproductive classes combined) moved a mean daily distance of 41 m (SE = 13.4, range = 13.3-128.1); males moved a mean daily distance of 55.4 m (SE = 26, range = 15-128); and females moved a mean daily distance of 26.7 m (SE = 4.5, range = 13-31).

Mean distance/move (magnitude) was analyzed for a total of 193 observations, 76 for four males, 79 for three gravid females, and 38 were for a single nongravid female (Table 2). For all 193 observations, the mean distance/move was 44.4 m (SE = 4.5, range = 0.4-458.9). For all observations (76), males moved a mean distance of 54.2 m (SE = 8.7, range = 0.4-458.9); gravid females moved a mean distance of 37.4 m (SE = 6.0, range = 1-280); and the single nongravid female moved a mean distance of 39.6 m (SE = 8.3, range = 0.5-185). After taking the average for each individual, Concho water snakes (sexes and reproductive classes combined) had a mean distance/move of 54.1 m (SE = 15.6, range = 20.4-153.7); males moved a mean distance of 67.4 m (SE = 30.4, range = 20.4–153.7); and females moved a mean distance of 40.9 m (SE = 9.6, range = 22.9-67). The mean movement distances of males and gravid females were not statistically different (one-tailed Mann-Whitney, $U_{1,2} = 6$, P = 0.57). Male Concho water snakes had a significantly greater percentage of movement days (64%; $\chi^2_1 = 4.04$, P < 0.05) compared to gravid females (43%); the single nongravid female moved on 57% of days tracked (Table 2). We were unable to implant transmitters and obtain telemetry data during peak mating activity in late April and early May, therefore the data were insufficient to be assessed seasonally.

Few movements greater than 50 m were recorded for any group (Table 2), suggesting strong site fidelity for both sexes. Gravid females were particularly sedentary. One female stayed in the same refuge for 30 d without any detectable movement, another female remained sedentary for 18 days. Females did occasionally make long movements. However, no significant difference existed in the number of movements over 50 m between males and gravid females ($\chi^2_1 = 0.02$, P > 0.5); nor did a difference exist in the actual distances moved over 50 m (Mann-Whitney, P > 0.05). The single nongravid female made nine movements greater than 50 m (Table 2).

Trap data provided additional information on movements. Five nontelemetered snakes, three males and two females, made emigration movements of approximately 800 m between adjacent habitats (Well Site #2 and Pecan Creek; Fig. 1). Four of these snakes moved from Pecan Creek to Well Site #2 during 1992, probably due to habitat reduction at Pecan Creek as a result of rising waters. The well sites at Spence provided a rocky shoreline regardless of the lake elevation.

Activity Range.—Concho water snakes at Spence had relatively small activity ranges (Table 3). A minimum of seven captures (based on graphical inflections of activity range) was necessary to adequately assess activity range for juvenile, gravid female, and adult male Concho water snakes.

Adult males had a mean activity range length of 278 m (\pm 90.8; N = 7); gravid females had a mean activity range length of 219 m (\pm 61.3; N = 7); and juveniles had a mean activity range length of 210 m (\pm 72.5; N = 4) (Table 3). A single nongravid, telemetered female (see Movements) had a mean activity range length of 271 m (\pm 15.5) (N = 51 location days); very similar to the mean activity range of adult males after seven captures (Table 3). Using only individuals with seven captures, there was no difference between male and gravid female activity range length (one-tailed Mann-Whitney, $U_1 = 23$, $U_2 = 26$, P = 0.64).

Telemetrically monitored gravid females did not select retreat sites farther from water than adult males ($t_s = 1.79$, P = 0.07). Males averaged 1.3 m from water (N = 4 snakes; SE = 0.1, range = 0–5), gravid females averaged 2.9 m from water (N = 4 snakes; SE = 0.4, range = 0–15). The single telemetered nongravid female averaged 2 m from water (SE = 0.4, range = 0–7.7).

DISCUSSION

The distribution of N. h. paucimaculata in Lake Spence was dynamic and strongly associated with the presence of rocky shoreline margins. The patchiness of available habitat combined with water level fluctuations appear to have driven the distributional variation observed in this study. Snakes were present in eastern and northern sections of the lake in 1987 when the water levels were high, but were apparently absent from these localities in 1990-1991 following a drop in lake surface elevation (Fig. 2). Evidence for a direct influence of water level fluctuation on snake habitat use was observed in 1992. An abrupt rise in water level and subsequent inundation of the Pecan Creek site resulted in the emigration of five resident adult N. h. paucimaculata to a neighboring well site.

Numerous studies have documented population level fluctuations for snakes. Such changes may be attributed to a variety of factors (see Dodd, 1987 for a listing). King (1986) reported on changes in the distribution and abundance of Nerodia sipedon insularum in Lake Erie, and listed human activity as the probable cause. He documented local extirpations for two islands in Lake Erie, although limited field work was conducted at one of them. Changes in the distribution of Concho water snakes at Spence, although local, appear to be driven by habitat alteration due to water level fluctuation (partially due to controlled releases to control chloride levels). The habitat stability afforded by well sites makes them important during lake fluctuations. Trapping and telemetry data revealed that snakes may either use them transiently on their way to other areas, or for extended periods of time. Well sites may be important refugia for snakes because they provide appropriate habitat at any lake surface elevation.

A growing number of studies are demonstrating the effects of sex, reproductive condition, and season on snake activity patterns (e.g., Viitanen, 1967; Secor, 1994; Charland and Gregory, 1995). Telemetry data collected between 1988– 91 for river populations revealed significant daily and seasonal differences between male and gravid female movements throughout the activity season (Greene, 1993). Our data hinted at such differences, but was insufficient to show a significant relationship.

The longest reported emigrational movement for a Concho water snake on the Colorado River was 14.9 km, for a male, over a three year period (Greene, 1993). The longest reported movement for a Concho water snake in a reservoir was 1600 m, for a male at Ballinger Lake. This compared to 800 m for five snakes (both sexes) at Spence. These five snakes moved between disjunct sites following a dramatic rise in water level and its resultant habitat alteration. Extensive dispersal movements by riverine snakes were relatively rare events or were not easily detected (Greene, 1993). The dynamic nature of habitat availability and size of Spence suggests a potential for dispersal movements of similar or larger magnitude to those recorded in other systems. However, long-distance movements at Spence could have been overlooked due to relatively low snake population densities and difficulty in sampling in this system (Whiting et al., 1996).

Linear activity ranges of adult N. h. paucimaculata at Spence were smaller than those in the Colorado River. Greene (1993) reported linear activity ranges of 434, 374, and 360 m for males, gravid females, and non-gravid females, respectively. Corresponding values for Spence were 287, 219, and 271. Despite the differences in mean activity range sizes among systems, the relative differences in activity range sizes among sexes were similar within each system. The riverine study sites used by Greene (1993) consisted of 800 m or more of continuous suitable habitat which could account for the larger activity ranges. We suggest that the apparent scarcity and patchiness of habitat at Spence may reduce spatial distributions of snakes relative to riverine populations.

Extrinsic factors such as habitat structure and resource availability may be the most important factors governing snake movement patterns. In temperate zone snakes, overwintering and feeding areas are often separated by large distances and require major migrational movements (Gregory et al., 1987). In the case of aquatic and semi-aquatic snakes, movements are often undertaken after a pond dries (Gregory et al., 1987). The long movements made by several Concho water snakes (0.8 km) between habitat patches may be described as emigrational movements due to shifting resource availability. Long movements often vary among snake populations, in the case of N. h. paucimaculata, long movements occur less frequently in river populations (Greene, 1993).

Although we did not quantify habitat availability relative to habitat use, it appears that the presence of rock was the most important structural feature guiding habitat selection processes in N. h. paucimaculata. Reinert (1993) suggested that structural cues relevant to habitat selection processes in snakes may be identified by examining intraspecific habitat selection patterns among geographic locations. Scott et al. (1989) reported that rock structures were a consistent distribution-wide correlate of N. harteri populations, including those inhabiting lake systems, an environment foreign to this taxon. Rocky shoreline alone, however, was not the sole predictor of Concho water snake presence. For example, the Spence dam (Fig. 1) was composed entirely of riprap rock, yet only diamondback (Nerodia rhombifer) and blotched (Nerodia erythrogaster transversa) water snakes were trapped on the dam. The substrate beneath the riprap was pea gravel, which was largely absent at other lake shore sites where Concho water snakes were found. Other factors such as water clarity, shoreline gradient, and wave action also may be important. Pecan Creek, where capture success was greatest, was characterized by turbid water, minimal wave action, a gentle gradient, a silt substrate, and a rocky shoreline. This site, in part by the nature of its location, most closely mimics the Colorado river habitat.

The apparent necessity of rocky beaches as a component of suitable lake habitat may be of considerable conservation importance as a foundation for habitat improvement efforts. The creation of new rocky beaches could create suitable habitat in previously unoccupied areas of lakes. Additionally, the quality of existing lake habitat could be improved by increasing the vertical distribution of rocky shorelines, thereby allowing persistence of suitable habitat over a wider range of lake surface elevations.

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Variation in Brown Snake (Storeria dekayi) Morphology and Scalation: Sex, Family, and Microgeographic Differences

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ABSTRACT.—Sex, family, and microgeographic variation in body size, head dimensions, tail length, and scalation were assessed from 273 wild-caught brown snakes (Storeria dekayi) from seven island and mainland sites near Lake Erie and from 145 neonates born to 25 wild-caught females. Significant differences between males and females were present both in wild-caught snakes and in neonates, with females exceeding males in snout-vent length and number of ventral scales and males exceeding females in tail length, head dimensions, and number of subcaudal scales. Previous analyses have typically focused on the effect that sex differences might have on adult snakes, e.g., in foraging or reproduction. The presence of sex differences among neonates raises the possibility that these differences may be of ecological and evolutionary significance in younger snakes as well. Significant differences among families were found in neonates for all characters except number of labial scales, and significant heritability (estimated from offspring-dam regression) was found for tail length, head length, and numbers of ventral, subcaudal, and temporal scales. Heritable variation in scalation is well known, but this is the first study to document heritable variation in snake morphology. This result is important because heritable variation is an implicit assumption of hypotheses for the evolution of sex, population, and species differences in morphology. Significant differences among sites were found for adult snout-vent length, head dimensions, number of subcaudal scales, and number of temporal scales. In addition, significant phenotypic correlations (e.g., among head dimensions, between tail length and number of subcaudal scales, between snout-vent length and number of ventral scales) and genetic correlations (e.g., between tail length and number of subcaudal scales, between head length and number of ventral scales) were found between pairs of traits. The presence of these correlations suggests that groups of traits may be influenced by the same genetic or ontogenetic processes and may exhibit patterns of correlated evolution.

Differences in morphology, behavior, or physiology between sexes, among age classes, or among localities may influence ecological relationships and reflect evolutionary trends. In snakes, sex differences in body size and relative head size may result in reduced diet overlap between males and females (Shine, 1991a; Houston and Shine, 1993) and geographic differences in body size and relative head size may reflect adaptation to local prey characteristics (Forsman and Lindell, 1993). Such hypotheses can be strengthened by an understanding of the genetic and ontogenetic processes giving rise to observed patterns of variation. For example, natural selection will result in sex or geographic differences only if traits show heritable variation. In addition, if multiple traits are genetically or ontogenetically correlated (e.g., if they are influenced by the same genes or by the same ontogenetic processes), then ecological or evolution-