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COLOR PATTERN POLYMORPHISM IN THE LAKE ERIE WATER SNAKE, *NERODIA SIPEDON INSULARUM*

Richard B. King
Department of Biological Sciences, Purdue University, West Lafayette, IN 47907

Abstract.—Populations of the water snake, *Nerodia sipedon,* on islands in western Lake Erie are polymorphic for color pattern. These populations include banded, intermediate, and unbanded morphs while surrounding mainland populations consist solely of the banded morph. The hypothesis that this polymorphism is maintained by strong selection and migration pressures is widely accepted. Unbanded morphs are apparently more cryptic along island shorelines while banded morphs are more cryptic on the mainland. Migration of banded morphs from the mainland explains their persistence in island populations.

Data collected in a capture-mark-recapture program on six islands provide no evidence of differential selection among morphs; morph frequencies do not differ among age classes, between once-captured and multiply-captured snakes, or between scarred and unscarred snakes. Furthermore, herring gulls, the most common snake predators in the island area, appear to detect banded and unbanded model snakes with equal ease. High site fidelity of water snakes and the distribution of morphs among islands suggest that migration from the mainland is not common. However, islands close to each other are similar in morph frequency, and water snakes have colonized islands elsewhere in the Great Lakes, indicating that some migration does occur. Recently, the frequency of banded morphs has increased in island populations while adult population sizes have declined. This increase in banded morphs is interpreted as reflecting an increased impact of migration from the mainland into these reduced populations.

One scenario for the evolution and maintenance of this polymorphism is that selection was important in establishing unbanded morphs in island populations as they became isolated from the mainland. As populations declined to their present size, the impact of migration from the mainland increased and is now swamping the effect of selection. Further declines in island population size may result in fixation of the banded morph.

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The discovery that large amounts of genetic variability exist in many natural populations has greatly influenced current views in evolutionary biology (e.g., Lewontin, 1974). Recent work centers on understanding the maintenance of this variability. Often a balance between evolutionary factors favoring alternative phenotypes is suggested, involving such mechanisms as selection and migration, temporal and spatial habitat heterogeneity, or recurrent mutation (Hedrick et al., 1976).

Color pattern polymorphism in Lake Erie island populations of the water snake, *Nerodia sipedon,* is commonly thought to result from a balance between natural selection and migration (Camin et al., 1954; Camin and Ehrlich, 1958; Ehrlich and Camin, 1960). Throughout most of its range in eastern and central North America, this snake is characteristically brown with dark crossbands and blotches along its entire length. However, populations on islands and the Catawba/Marblehead Peninsula of western Lake Erie contain a high frequency of uniformly gray, unbanded individuals and a variety of intermediates in addition to banded individuals (Conant and Clay, 1937). The unbanded morph is common only in the island area of western Lake Erie, and populations containing it are designated *Nerodia* (=*Natrix*) *sipedon insularum* (Conant and Clay, 1937, 1963).

The influence of migration on this polymorphism was first suggested by Conant and Clay (1937), who concluded that intermediate and banded individuals exist in the island populations because of migration from mainland populations which are 1–20 km away. The first evidence that selection influences this polymorphism was provided by Camin et al. (1954). They found that the frequency of the banded morph was significantly lower among adults than among juveniles and attributed this difference to differential predation. Water snakes on islands are found mostly on exposed limestone and dolomite shorelines, while on the mainland they exist in more overgrown habitats such as marshes, ponds, and streams. Due to these habitat differences, the unbanded morph may be more cryptic to visual predators on islands, while the banded morph may be more cryptic on the mainland. Camin and Ehrlich (1958) and Ehrlich and Camin (1960) further supported the selection-migration hypothesis by demonstrating a significantly higher frequency of banded morphs in island litters than among adults. These authors conclude that pattern polymorphism in Lake Erie water snakes is maintained by a "balance between strong selection and migration pressures" (Camin and Ehrlich, 1958 p. 510). These studies have since become widely cited for providing an example of a polymorphism maintained by such a balance (e.g., Ford, 1975; Stebbins, 1977; Futuyma, 1979).

The conclusion that selection and migration act to maintain pattern polymorphism in Lake Erie water snakes is perhaps premature. First, there is only circumstantial evidence that water snakes migrate between the mainland and islands. Camin and Ehrlich (1958) report that water snakes were seen "swimming several miles from the nearest shore" (p. 507), but actual instances of successful migration are unknown. Second, there are few data to indicate that differential predation is the agent of selection responsible for the difference in morph frequency between newborn and adult snakes. Gulls (Laridae), herons (Areidae), and raptors (Falconiformes) are thought to be the most important snake predators in the area (Camin et al., 1954; Camin and Ehrlich, 1958), but these birds may rarely attack snakes; only one water snake was found in the stomachs of nearly 800 herons and gulls (Ligas, 1952; Hoffman and Curnow, 1979; Jarvis and Southern, 1976).

In this study, I set out to determine whether: 1) age-specific differences in morph frequency observed by previous investigators occur in present populations; 2) recapture data are consistent with the hypothesis of differential survival among morphs; 3) morphs differ in the frequency of scars which might be indicative of predation attempts; 4) avian predators detect banded morphs more easily than unbanded morphs; 5) the distribution of morphs among islands reflects that expected if migration from the mainland is common; and 6) morph frequencies are stable through time. Data were gathered in a five-year field investigation and a survey of preserved specimens of water snakes from the Lake Erie area.

MATERIALS AND METHODS

Independence of Morph and Age.—A capture-mark-recapture program was conducted from 1980–1984 at 12 sites on six islands: Pelee, Middle, Kellys, North Bass, Middle Bass, and Johnsons (Fig. 1). Data collected include age class (young-of-the-year, juveniles one to three years old, and adults determined from size-frequency distributions), sex, year of study, and morph (see King, 1985, 1986 for details of site selection and data collection). Color pattern was scored as follows (Fig. 2). Banded snakes had dorsal and lateral blotches at regular intervals along their entire length and most lateral blotches occupied six or more scale rows. Anterior lateral and dorsal blotches joined to form saddles on many banded individuals but on others, anterior blotches were reduced to fewer than six scale rows. Intermediate snakes showed less extensive patterning and dorsal blotches were fre-

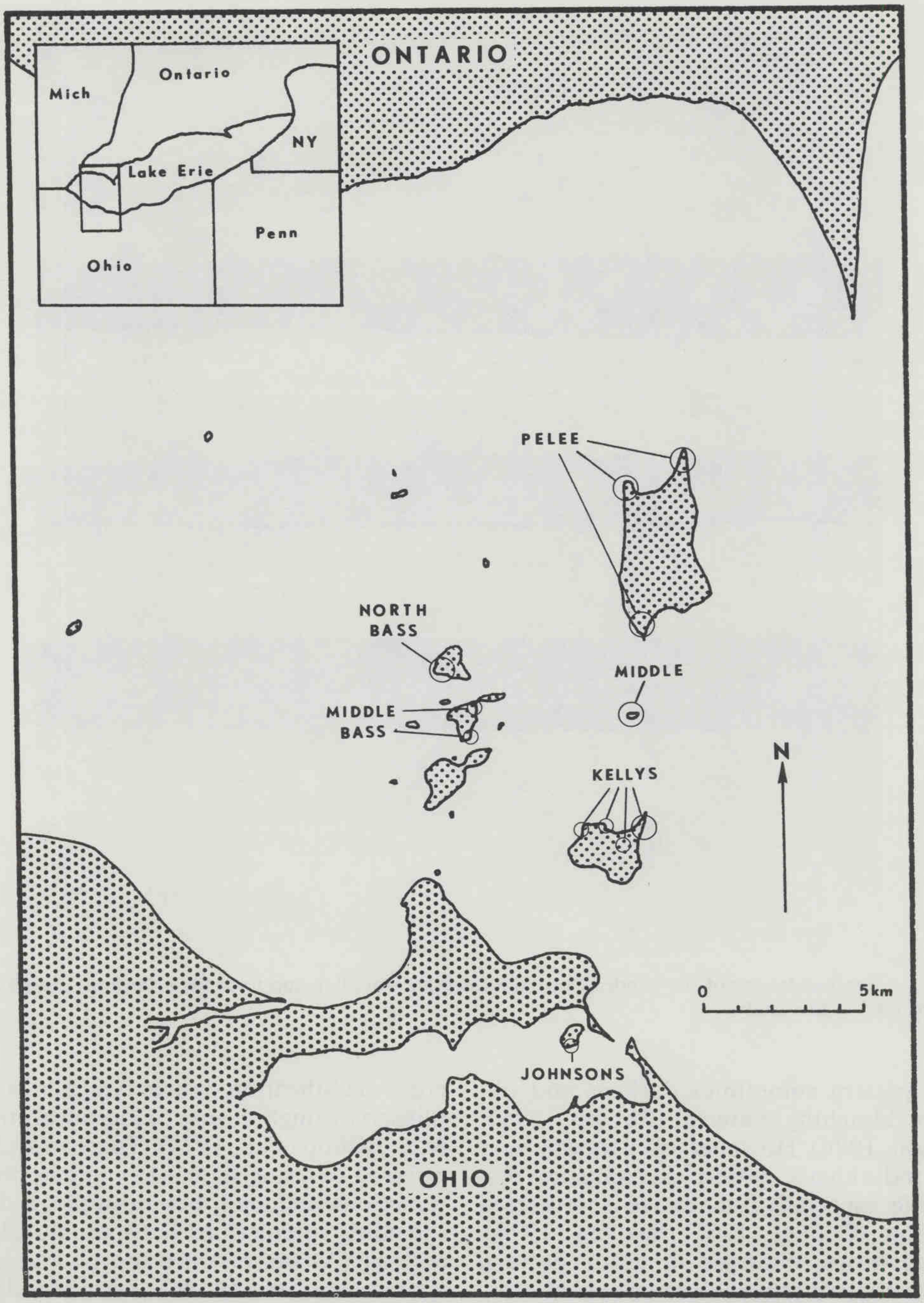

FIG. 1. The west end of Lake Erie showing islands included in this study.

quently absent posteriorly or irregular in shape. Lateral blotches were often absent anteriorly and most occupied fewer than five scale rows resulting in a lateral stripe for at least part of the length of the snake. Unbanded snakes lacked all dorsal and lateral patterning or had faint dorsal blotches anteriorly and lateral blotches not extending higher than scale row 3.

As adult water snakes continue to age,

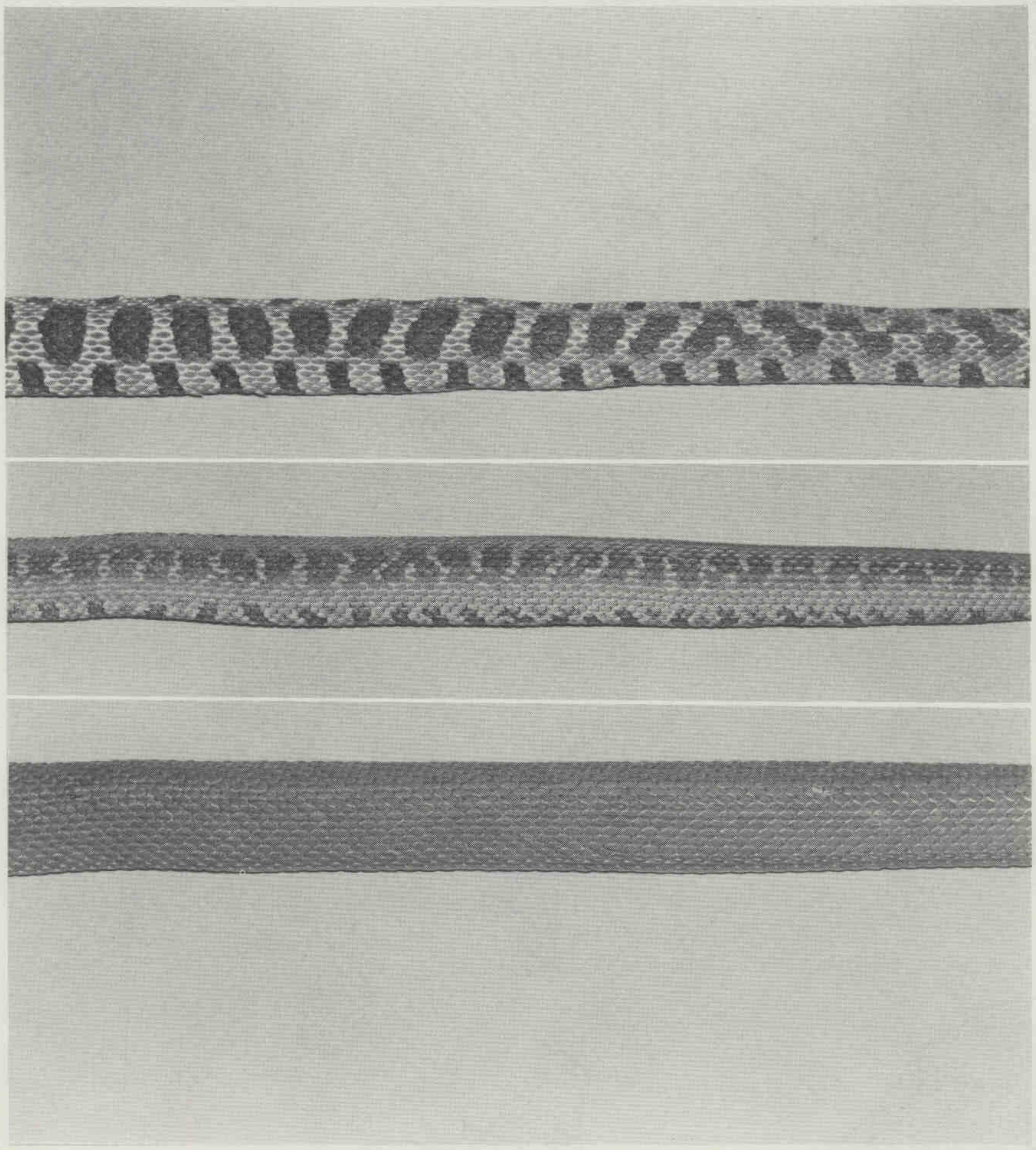

FIG. 2. Representatives of the banded (top), intermediate (middle), and unbanded (bottom) morph classifications used in this study.

color pattern sometimes darkens and obscures blotching pattern (Conant, 1951; Beatson, 1976). However, even among very dark individuals, pattern elements are discernible, especially if the snake is immersed in water (Conant, 1951; Beatson, 1976). Furthermore, changes in color pattern among captive snakes does not affect scoring (Camin and Ehrlich, 1958), even from birth to an age of six years (pers. observ.). Banded morphs appear distinctly banded as young-of-the-year, as juveniles, and frequently as adults.

Testing for independence between morph and age is complicated by the fact that snakes are also classified by site, island, sex, and year. Analysis of such multi-dimensional cross-classification data is typically accomplished through the use of log-linear models (e.g., Bishop et al., 1974). These models are referred to using letters to indicate the interactions included. For example, a model including interactions between morph (M) and age (A) and between morph and island (I) is designated MA, MI. Tests of independence are based on comparisons of the fit obtained with models containing or lacking a particular interaction (see Appendix).

Islands were initially analyzed separately to determine if years, sites, and sexes could be pooled within islands (see Appendix for pooling criteria). Morph or age were independent of year, site, and sex on all islands except Pelee where both were dependent on year (raw data in King, 1985). However, no directional influence of year on morph was noted during the four years Pelee Island was censused. Therefore, years, sites, and sexes were pooled within islands and the resulting three-way classification table of pattern, age, and island was used to test for independence of morph and age.

Morph frequencies of 39 litters from four islands were obtained by keeping gravid females captive until parturition. Testing for independence of morph and age using these data is difficult because littermates are genetically related and therefore violate the assumption of statistical independence. My solution was first to treat littermates as independent samples. If no significant differences can be found among age groups based on this assumption, more conservative tests will also be nonsignificant. A similar test was made treating littermates as non-independent samples by using the proportion of each morph within litters. If this test is significant, there can be little doubt that significant differences in morph frequency occur among age groups.

Independence of Morph and Capture Status.—The effect of morph on survivorship was assessed by classifying snakes as once-captured or multiply-captured (captured in more than one field season). Snakes marked during the final field season of study at a particular site were not included because they had no chance of being recaptured. Young-of-the-year and juveniles were also excluded because they were rarely recaptured; hence, their inclusion would reduce the chance of detecting differences in capture rate among adults. Independence of morph and capture status was tested using log-linear analysis of the four-way classification table of morph, capture status, sex, and island.

To test for independence of morph and capture status specifically among young-of-the-year, 317 newborns were released en masse on Middle Bass Island. These were offspring of wild-caught females from that island and adjacent North Bass Island and were released soon after birth in the fall of 1983. Such local concentrations of newborns occur naturally following birth in fall and following emergence from hibernation in spring. The release area and suitable contiguous habitat (about 250 m of shoreline) was searched intensely the following spring and summer for these snakes. A *G*-test was used to compare morph frequency between those snakes subsequently recaptured and those not recaptured (Sokal and Rohlf, 1981).

Independence of Morph and Scar Status.—Snakes were scored in the field for the presence of scars or stub tails which may have resulted from failed predation attempts. Analysis was restricted to juveniles and adults because few young-of-the-year were scarred. Both sex and island were independent of either pattern or scar status so sexes and islands were pooled. A *G*-test was then used to compare morph frequency among snakes differing in scar status.

Morph Detection Experiment.—Model snakes were employed to determine if herring gulls, *Larus argentatus,* detected banded or unbanded morphs more readily. This experiment was conducted on Middle Island because of its high density of herring gulls (Mineau and Markel, 1981). Two types of models were used: rubber imitation earthworms, and wax or plaster casts of an actual water snake made using a latex mold. Rubber earthworms were 20 cm in length and corresponded in size to newborn water snakes. Casts measured 45 cm and were modeled on an 18-month-old snake. Both types of models were sigmoid in shape. Unbanded morphs were painted uniformly gray-brown, and banded morphs were painted with dark brown dorsal and lateral blotches on a gray-brown background. Colors were chosen to match live snakes (King, 1985). Morphs were divided evenly among rubber, wax, and plaster models.

In each of 30 runs of the experiment, models were placed at 3–5 m intervals along shorelines used by both water snakes and herring gulls. Models were placed in natural basking positions conforming to the contours of the shore. Order of morphs was determined by coin toss. Models were scored as attacked or not attacked 2–4 hours after placement (or the following morning for those models distributed in the evening). Attack status was based on disappearance, breakage, or displacement of models. Attacks could be attributed to herring gulls because beak marks were often apparent on attacked models and other avian predators were not seen along the shoreline where experiments were conducted. Up to 96 models were deployed per run. Successive runs of the experiment were made by moving each model 3–5 m down the shore. Independence of morph and attack status was tested using log-linear analysis of the three-way classification table of morph, attack status, and size.

Distribution of Morphs Among Islands.—Camin and Ehrlich (1958) suggested that morph frequency should differ among islands because distant islands receive fewer mainland migrants than nearby islands. However, migration among the islands themselves will act to reduce these differences. The relative importance of mainland versus island migrants depends on the position of each island in relation to both the Ohio and the Ontario mainland and to other islands. Source population size should also influence migration; large populations may produce more migrants than small ones. The area of the recipient island and its population size should also influence the impact of migration, but these effects will be the same whether migrants come from the mainland or from other islands. A number of indices assessing the impact of migration on morph frequency can be devised based on these parameters. The index described below is based on the ratio of migration from the mainland to migration from other islands assuming that migration rate is a reciprocal function of distance. For a given island, this ratio can be written in terms of M_i, the mainland population size required to balance the effect of migration among islands, by assuming that the Ohio and Ontario mainland water snake populations are equal:

$$M_i = \frac{\sum_j \frac{N_j}{D_{ij}}}{\sum_k \frac{1}{D_{ik}}}$$

where:

N_j = size of the jth island source population,
D_{ij} = distance from the ith island to the jth island, and
D_{ik} = distance from the ith island to the kth mainland (Ohio or Ontario).

Islands having high index values are expected to be influenced more by migration from other islands, while islands having small values are expected to be influenced more by migration from the mainland. Values of M_i were calculated for each island using estimates of adult water snake population sizes obtained in this study (King, 1985, 1986), and distances among the islands and the mainland were estimated from NOAA chart #14830. The impact of migration was estimated by examining the correlation between these values and morph frequencies of adult water snakes.

Movements of marked individuals were also used to determine the likelihood of migration. It was not feasible to mark large numbers of mainland snakes to detect migration from the mainland to the islands. However, movements of marked snakes within the island study area were monitored to indicate the potential for long distance migration. In addition, movement patterns of young-of-the-year were determined from the mass release experiment described previously.

Changes in Morph Frequency Through Time.—Rough comparisons of morph frequency were made through time by lumping morph categories used in previous studies and comparing their frequencies with those in this study. Unbanded, intermediate, and banded morphs in this study correspond approximately to type A, types B and C, and type D, respectively, described by Conant and Clay (1937). The seven categories of Camin et al. (1954) correspond as follows: A and ab = unbanded; B, bc, and C = intermediate; and cd and D = banded. To document changes in morph frequency through time more rigorously, I scored 1,118 museum specimens of water snakes from the Lake Erie area. Many specimens were from captive-born litters and hence could not be considered independent samples. Analysis was therefore restricted to 128 wild-caught individuals older than one year (>27 cm snout–vent length, King, 1985, 1986) from sites with sizable samples (7–33 snakes) collected over relatively short time intervals (3–13 years) (raw data in King, 1985).

TABLE 1. Frequencies of morphs among age groups of water snakes on six islands in Lake Erie. Young-of-the-year are designated YOY. Morph abbreviations are u = unbanded, i = intermediate, and b = banded. Model MI, AI: $G = 23.39$, $P = 0.50$, $d.f. = 24$. Model MI, AI, MA: $G = 16.09$, $P = 0.71$, $d.f. = 20$. Effect of MA: $G = 7.30$, $P = 0.12$, $d.f. = 4$. M, A, and I refer to morph, age, and island, respectively.

		Morph		
Island	Age	u	i	b
Pelee	YOY	5	20	34
	Juvenile	10	32	36
	Adult	20	80	71
Middle Bass	YOY	24	78	50
	Juvenile	3	17	13
	Adult	19	50	33
Kellys	YOY	0	4	2
	Juvenile	4	9	6
	Adult	20	47	29
North Bass	YOY	10	56	29
	Juvenile	16	28	15
	Adult	53	119	53
Middle	YOY	0	2	1
	Juvenile	1	0	0
	Adult	6	6	15
Johnsons	YOY	0	2	1
	Juvenile	0	0	0
	Adult	3	14	31

TABLE 2. Frequencies of morphs among newborn and adult water snakes on four islands in Lake Erie. Morph abbreviations are as in Table 1. A. Litter-mates treated as independent samples. Model MA, MI: $G = 14.77$, $P = 0.10$, $d.f. = 9$. Model MI, A: $G = 33.94$, $P < 0.001$, $d.f. = 11$. Effect of MA: $G = 19.17$, $P < 0.001$, $d.f. = 2$. M, A, and I refer to morph, age, and island, respectively. B. Litter-mates treated as non-independent samples. Number of litters is shown in parentheses. Model MI, A: $G = 2.99$, $P = 0.99$, $d.f. = 11$. Model MI, MA: $G = 2.23$, $P = 0.99$, $d.f. = 9$. Effect of MA: $G = 0.77$, $P = 0.68$, $d.f. = 2$.

		Morph		
	Island	u	i	b
Adults	Middle Bass	19	50	33
	North Bass	53	119	53
	Kellys	20	47	29
	Johnsons	3	14	31
A.				
Litters	Middle Bass	20	116	52
	North Bass	60	225	155
	Kellys	24	75	61
	Johnsons	1	56	69
B.				
Litters	Middle Bass (10)	1.1	6.3	2.6
	North Bass (18)	2.5	9.4	6.1
	Kellys (7)	1.0	3.3	2.7
	Johnsons (4)	0.0	1.5	2.4

Groups collected from given sites at different times were then compared among themselves and with field samples collected in this study using G-tests to determine if morph frequencies changed through time.

RESULTS

Independence of Morph and Age.—In the field, 1,177 water snakes were classified by morph (M), age (A), and island (I) (Table 1). These data were fit with the log-linear model including the morph-by-island and the age-by-island interactions (MI, AI). To test the null hypothesis that morph and age were independent, this fit was compared with that obtained with the model which included the morph-by-age interaction (MI, AI, MA). The difference between models was not significant ($G = 7.30$, $P = 0.12$, $d.f. = 4$), indicating that morph and age are independent (Table 1). The inclusion of the MI and AI interactions in the model indicate that morph and age distributions differed among islands.

Morph frequencies of adults were compared to those of 914 newborns born to 39 wild-caught females from four islands. When littermates were treated as independent samples (Table 2A), the null hypothesis that morph and age were independent was rejected ($G = 33.94$, $P = 0.0004$, $d.f. = 11$). This was due mostly to a higher frequency of banded morphs among newborns than among adults from North Bass Island. Morph was independent of age on each of the other islands when they were considered singly. When littermates were treated as non-independent samples (Table 2B), the null hypothesis was not rejected ($G = 0.77$, $P = 0.68$, $d.f. = 2$). Thus, conclusions about the independence of morph and age depend on the degree of independence among littermates.

Independence of Morph and Capture Status.—About 15% of adult snakes were captured more than once during this study. The null hypothesis that morph and capture status were independent was not rejected ($G = 0.44$, $P = 0.80$, $d.f. = 2$), suggesting that adult survivorship did not differ among

TABLE 3. Frequencies of morphs among once-captured and multiply-captured adult water snakes on six islands in Lake Erie. Morph abbreviations are as in Table 1. Model MX, MI, CX, CI: $G = 42.41$, $P = 0.54$, *d.f.* = 44. Model MX, MI, CX, CI, MC: $G = 41.97$, $P = 0.47$, *d.f.* = 42. Effect of MC: $G = 0.44$, $P = 0.80$, *d.f.* = 2. M, I, X, and C refer to morph, island, sex, and capture status, respectively.

			Morph		
Island	Sex	Capture status	u	i	b
Pelee	male	once	7	36	29
		multiply	0	1	4
	female	once	5	22	19
		multiply	1	4	0
Middle Bass	male	once	5	22	9
		multiply	0	1	1
	female	once	6	15	11
		multiply	2	3	1
Kellys	male	once	8	14	7
		multiply	1	4	1
	female	once	7	16	12
		multiply	0	4	2
North Bass	male	once	21	59	21
		multiply	3	11	5
	female	once	11	18	16
		multiply	10	7	4
Middle	male	once	3	4	6
		multiply	0	0	1
	female	once	3	1	4
		multiply	0	1	4
Johnsons	male	once	1	10	12
		multiply	0	0	3
	female	once	2	3	15
		multiply	0	1	0

morphs (Table 3). The inclusion of the capture status-by-sex interaction in the model probably occurred because male and female water snakes are not equally likely to be caught (Feaver, 1977). The inclusion of the capture status-by-island interaction in the model probably resulted from differences in snake density and capture effort among islands.

Capture status appears to be independent of morph among young snakes as well. Of the 317 newborns released on Middle Bass Island, 56 were recaptured the following spring and summer. Searches at more distant sites on this same island and on other islands produced none of these snakes. Frequencies of unbanded (u), intermediate (i), and banded (b) snakes later recaptured (6u, 35i, 15b) were compared with those not recaptured (23u, 155i, 83b) using a G-test. The null hypothesis that capture status and morph were independent was not rejected ($G = 0.64$, $P = 0.73$, *d.f.* = 2), providing no evidence of differential survivorship among morphs.

Independence of Morph and Scar Status.—Nearly 17% of juvenile and adult snakes had obvious scars or tail stubs. Morph frequencies were compared between scarred (27u, 56i, 51b) and unscarred (112u, 322i, 223b) snakes using a G-test. The null hypothesis that scar status and morph were independent was not rejected ($G = 2.38$, $P = 0.30$, *d.f.* = 2), suggesting that predation attempts which resulted in scars or stub tails occurred with equal frequencies among morphs.

Morph Detection Experiment.—A total of 361 unbanded and 368 banded model juvenile presentations, and 272 unbanded and 254 banded model newborn presentations were made to assay differential ability of gulls to detect banded and unbanded morphs. Of these, 37 unbanded and 34 banded juveniles and 27 unbanded and 25 banded newborns were attacked. The null hypothesis that attack status and morph were independent was not rejected ($G = 0.14$, $P = 0.71$, *d.f.* = 1). Thus, morphs did not differ in the degree to which they were detected by herring gulls.

Distribution of Morphs Among Islands.—According to the migration index described above, Johnsons Island was expected to have the most banded morphs and Middle Island the fewest. M_i did show a significant correlation with morph frequency but only for the unbanded morph (Table 4B). No significant correlations were found between morph frequency and two other migration indices: distance to the nearest mainland point, and a version of M_i which assumes migration rate is a reciprocal function of distance squared.

This analysis addresses only the relative importance of migration from the mainland and from other islands and not the actual rate of migration. However, recaptures of marked snakes within the study area provide data on movement patterns. Two hundred two snakes were recaptured 2–1,146 days after initial capture. All were

TABLE 4. A. Migration index values for six islands in Lake Erie. B. Correlation coefficients between index values and morph frequencies of adult water snakes. Morph abbreviations are as in Table 1.

A. Island	M_i
Johnsons	60.8
Kellys	445.3
Middle Bass	2,037.9
North Bass	1,678.6
Pelee	584.5
Middle	2,051.9

B. Pearson correlation coefficients

Morph		
u	i	b
0.72	0.01	−0.33
$P = 0.05$	$P = 0.50$	$P = 0.26$

TABLE 5. Changes in morph frequency through time. A. Comparisons using published data (modified from Conant and Clay, 1937; Camin et al., 1954; see text for details). B. Comparisons using data on preserved specimens. Morph abbreviations are as in Table 1.

Island	Date	Morph u	Morph i	Morph b
A.				
Kellys	pre-1937	2	12	2
	1980–1983	20	47	29
Middle Bass	pre-1937	14	32	5
	1981–1984	19	50	33
Pelee	pre-1937	22	14	0
	1980–1983	20	80	71
Middle	1949	89	33	9
	1980–1983	6	6	15
B.				
Pelee	1933–1937	9	9	3
	1947–1950	14	14	5
	1959–1961	1	3	3
	1980–1983	20	80	71
$G = 27.61$, $P = 0.0001$, $d.f. = 2$.				
Middle	1945–1958	8	7	1
	1980–1983	6	6	15
$G = 14.22$, $P = 0.0008$, $d.f. = 2$.				
South Bass	1893–1901	2	4	3
	1930–1940	10	10	1
	1948–1953	6	12	3
$G = 5.33$, $P = 0.26$, $d.f. = 2$.				

found within about 300 m of the original capture site and many were within 50 m. No snakes were observed to move between islands or between sites within islands even though these distances were as short as 1.3 km. Recaptures of snakes in successive field seasons can be used to estimate an upper limit on annual migration rate among study sites. Ninety-nine snakes were recaptured 1, 2, or 3 years after marking, for a total of 128 snake-years. A 95% confidence interval for the proportion migrating per year (0/128) has an upper limit of 3%. Because distances from the mainland are typically greater than among island study sites, immigration from the mainland presumably occurs at an even lower rate. Snakes swimming offshore were followed for distances as great as 100 m parallel to the shore. Longer distance movements may take place, but site fidelity appears high. Movements of newborns in the mass release experiment described above also indicate high site specificity. Recaptures were mostly restricted to within 25 m of the release point. The one exception was an individual recaptured 50 m from the release site. Unlike older snakes, which were recaptured throughout the active season, newborns were recaptured mostly in spring and early summer. Thus, dispersal may be underestimated in this age class.

Changes in Morph Frequency Through Time.—Morph frequencies of island populations of Lake Erie water snakes have changed in this century. Qualitative comparisons between published data and data collected here indicate that on four islands (Kellys, Middle Bass, Pelee, and Middle Island) the banded morph has increased by 18–49%, while the unbanded morph has decreased by 8–53% over a span of 31 to 43 years (Table 5A).

Comparisons among collections of preserved snakes corroborate these results for two of the islands above. Significant differences in morph frequency were found among four samples from Pelee Island: preserved snakes collected in 1933–1937, 1947–1950, and 1959–1961, and field data from 1980–1983; and between two samples from Middle Island: preserved specimens collected in 1945–1958 and field data from 1980–1983 (Table 5B). On both Pelee and Middle Island the frequency of the banded morph has more than doubled over the time period sampled. On Pelee Island, this change appears to have taken place since 1950. Samples collected there in 1933–1937 and 1947–1950 are essentially identical in morph frequency ($G = 0.13$, $P = 0.94$, $d.f. = 2$), but differ from the 1980–1983 sample ($G = 20.07$, $P < 0.0001$, $d.f. = 2$). The 1959–1960 sample did not differ from earlier samples ($G = 3.68$, $P = 0.45$, $d.f. = 2$) or from the 1980–1983 sample ($G = 0.11$, $P = 0.95$, $d.f. = 2$). In contrast to these islands, no significant differences in morph frequency were found among three samples of preserved snakes collected on South Bass Island in 1893–1901, 1930–1940, and 1948–1953 (Table 5B). These comparisons assume that museum collections represent random samples of water snake morphs. If unbanded morphs were collected preferentially, increases in the banded morph would be overestimated. However, museum collections appear to contain the same or fewer unbanded morphs than published frequencies for the same islands and time periods (compare Table 5A and B) suggesting this is not a problem.

DISCUSSION

Natural Selection of Color Pattern.—Comparisons of morph frequency among wild-caught snakes of different ages, between once-captured and multiply-captured snakes, and between scarred and unscarred snakes provide no evidence that differential mortality occurs among morphs at present. This finding is further supported by recapture rates among morphs of captive-born snakes released in the field. In addition, herring gulls appear to detect banded and unbanded model snakes with equal ease. Only the comparison of morph frequency between captive-born litters and wild adults suggests selection may occur, and here conclusions depend on how the problem of statistical independence among littermates is treated. If selection is occurring in present Lake Erie water snake populations, it is not "strong" as Camin and Ehrlich (1958) postulated. Weak selection may have gone undetected in my analysis, but assuming that the intermediate morph occurs at the same frequency among young-of-the-year and juveniles as among adults on a given island, consistent differences of less than 4% in the frequency of the other morphs would be significant ($\alpha = 0.05$) given my sample sizes. Tests comparing attack frequency among model snake morphs have similar statistical power.

How can the observation that selection on color pattern in Lake Erie water snakes is currently weak or absent be reconciled with the conclusions of earlier investigators that selection is strong? One possibility is that the intensity of predation on the banded morph varies through time. Changes in predator faunas have occurred during this century, but their impact on water snake populations is difficult to assess. Some snake predators (e.g., bald eagles) are now rare in the island region; others (e.g., herring gulls) have increased dramatically; and still others (e.g., herons) have become rare on some islands but have increased on other islands (King, 1985). Unfortunately, it is difficult to determine whether these changes have either increased or decreased the intensity of predation on water snakes in general or on the banded morph in particular. Current gull and heron distributions do not appear to correlate with water snake morph frequencies in the expected direction; Middle Island, which has high densities of these birds also has a high frequency of banded morphs.

Another explanation for the difference between my findings and those of previous investigators may lie in methods of data collection and analysis. As noted above, data analyzed by Camin and Ehrlich (1958) and Ehrlich and Camin (1960) were collected over a long time span. In particular, samples of litters were collected in 1948, 1957, and 1958 while the bulk of adult snakes were collected prior to 1937. Thus, differences in morph frequency between age classes may be attributable to selection as these authors suggest or they may reflect nonselective changes in morph frequency through time. The fact that changes in morph frequency between the 1930's and the present can be documented, and that the banded morph has increased in frequency over this period, lends credence to this latter possibility. Data from museum specimens allows comparison of morph frequency between litters and adults collected at the same time. By scoring morphs dichotomously (A and B = unbanded, C and D = banded), Camin and Ehrlich (1958) found a difference of 0.54 in the frequency of the most banded morphs between litters and adults from the "Bass Complex." However, I found differences of only 0.29 for samples collected on South Bass Island in 1937–1939 (212 newborns from an unknown number of litters compared with 21 adults), and 0.28 for samples collected there in 1948–1953 (242 newborns from 13 litters compared with 21 adults) (intermediates were divided evenly between banded and unbanded categories for these comparisons).

The work of Camin et al. (1954) is free of temporal bias because juvenile and adult snakes were collected at the same time. Interestingly, if these snakes are classified dichotomously, morph frequencies differ by only 0.17 between age groups. However, the juvenile age class consists entirely of snakes born the previous fall (Camin et al., 1954), and many came from a single site: "an old well . . . about 5 feet square" (Triplehorn, in Conant, 1951 p. 237). As noted in the mass release experiment described above, newborn snakes apparently move only short distances during their first months of life. Thus, it is possible that many of these individuals were littermates who had not dispersed since birth and do not represent independent samples. This criticism can also be leveled against data collected in this study; my captures of young-of-the-year were also clumped in time and space. However, the fact that I conducted field work over a five-year period and at a number of sites should minimize this effect.

In snakes, adaptive interpretations of color pattern frequently center on its function in crypsis (Beatson, 1976; Jackson et al., 1976; Pough, 1976; Bechtel, 1978; Zweifel, 1981; Vincent, 1982; Sweet, 1985), although thermoregulation, warning coloration, and mimicry are apparently important in some species (Gibson and Falls, 1979; Greene and McDiarmid, 1981). Blotched patterns are typically thought to make stationary snakes cryptic against mottled backgrounds while uniform and striped patterns are thought to make moving snakes appear stationary (Jackson et al., 1976; Bechtel, 1978; Zweifel, 1981).

The effect of pattern variation on crypsis within populations has been investigated only rarely. Water snakes (*Nerodia sipedon*) in Kansas, exhibit high heritabilities for dorsal and lateral blotch numbers (0.62 and 0.38, respectively), and selection for crypsis apparently favors increased blotch numbers (Beatson, 1976). In dimorphic populations of Lake Erie area garter snakes (*Thamnophis sirtalis*), melanistic morphs apparently thermoregulate more effectively than striped morphs but are less cryptic to predators (Gibson, 1978). In both of these studies conclusions regarding differential predation are based on differences in scar or tail stub frequencies among snakes differing in pattern. However, such differences can result from either differences in predator intensity (predators attack certain morphs more often) or predator efficiency (attacks on certain morphs are more often successful) (Schoener, 1979; Jaksic and Greene, 1984). In the first case, less cryptic snakes are expected to exhibit higher scar frequencies than more cryptic snakes, while in the second case, less cryptic snakes are expected to exhibit lower scar frequencies than more cryptic snakes. Thus, conclusions about the direction of selection depend on which of these causes is responsible for differences in scar or tail stub frequencies.

Migration Among Island and Mainland Populations.—The correlation between the frequency of the unbanded morph and the migration index M_i suggests migration from the mainland does have some influence on morph frequency among islands. The lack of a correlation with the frequency of the banded morph is somewhat puzzling. However, the island closest to the mainland, Johnsons Island, does have the highest frequency of the banded morph. Furthermore, North Bass and Middle Bass Island, which are separated by only 1.3 km do not differ significantly in adult morph frequency ($G = 2.99$, $P = 0.22$, *d.f.* = 2), while islands more distantly separated from each other, such as North Bass and Pelee Island (10.7 km apart), do differ in morph frequency ($G = 18.40$, $P = 0.0001$, *d.f.* = 2). In contrast with morph frequencies, frequencies of protein polymorphisms are virtually identical among all island and mainland populations sampled (King, 1985). This may result from migration among island and mainland populations or may reflect the recent origin of the island populations (King, 1985).

The high site fidelity of water snakes observed in this study has been reported by others as well (Blanchard and Finster, 1933; Brown, 1940; Fraker, 1970), and homing behavior has been observed following displacements of up to 600 m (Fraker, 1970). Longer movements (up to several km) have been reported (Blanchard and Finster, 1933; Brown, 1940), but may be restricted to large individuals. Young-of-the-year (18.1–18.8 cm SVL) become exhausted after an average of 5.1 min of continuous activity, while adults (>60 cm SVL) can remain active for an average of 42.0 min (Pough, 1978), and can remain afloat for more than eight days (Brown, 1940).

Adult water snakes could certainly survive a crossing from the mainland to the islands. The presence of water snakes on islands in Georgian Bay, Ontario (Schueler, unpubl.) indicates their ability to colonize island habitats. Unlike islands in Lake Erie, which are land-bridge islands isolated from the mainland by rising lake levels (Lewis, 1969; Forsyth, 1973), many of the islands in Georgian Bay appeared as lake levels subsided and were never part of the mainland (Schueler, unpubl.). Water snakes now found on these islands must be descended from colonists who crossed the 3–4 km water barrier from the mainland. However, water snakes are absent from a number of islands elsewhere in the Great Lakes despite the presence of apparently suitable habitat on them (Hatt et al., 1948; Long and Long, 1976; Schueler, unpubl.). In addition, they have failed to recolonize West Sister Island in Lake Erie, though they were found there as recently as 1938 (King, 1985, 1986). This island is 14 km from the nearest mainland point, making it one of the most isolated islands in Lake Erie. Thus, while levels of migration may be sufficient to maintain high genetic similarity in proteins among Lake Erie island and mainland populations of water snakes, they are not sufficient to be reflected in the movements of marked snakes and may have only a small effect on variation in morph frequencies among islands.

Maintenance of Color Pattern Polymorphism.—The observation that present selective pressures on color pattern are weak at best, indicates that if migration from the mainland is excessive, this polymorphism may be transitory and island populations will become dominated by the banded morph in the future. Recent increases in the frequency of the banded morph may reflect such a process. Declines in island water snake populations in this century (King, 1985, 1986) may have increased the influence of migration from mainland populations. Population sizes are now on the order of tens to hundreds of adults per island, but have remained high in protected marshes on both the U.S. and Canadian mainland. Further declines in island populations may result in fixation of the banded morph.

In light of these findings, I propose a scenario for the origin and maintenance of this polymorphism. As noted above, the islands did not become isolated from the mainland until Lake Erie rose to near its present level about 4,000 years ago. However, pollen and isotope studies indicate that climate approached present conditions between 7,000 and 8,000 years ago (Fritz et al., 1975). This suggests that water snakes inhabited the island region prior to isolation, rather than secondarily colonizing the islands following isolation. This view is supported by distributional patterns of other reptile species in the island region (King, 1987). Prior to isolation, gene flow between future island and mainland populations was presumably high, and exposed shore-like habitats were rare, making any selection for the unbanded morph ineffective. As the islands became isolated, gene flow decreased. With rising lake levels, the exposed rocky island shorelines became suitable water snake habitat. Under such conditions, selection favoring the unbanded morph, however weak, may have been effective. Unbanded morphs probably arose through mutation since they have been reported occasionally from water snake populations elsewhere (e.g., Pennsylvania, Virginia, and West Virginia: Conant and Clay, 1937; Missouri: Nickerson and Krager, 1975; Cape Cod: Lazell, 1976). The large size of former island water snake populations increased the chance that such a mutation could have occurred, and also served to buffer island populations against the effect of migration from the mainland. However, as island populations declined to their present size, the impact of migration from the mainland increased and is now swamping the effect of selection. Under this scenario, the relative importance of selection and migration on this polymorphism varies through time. Selection is important in the establishment of unbanded morphs in island populations. Migration from the mainland is important in the recent increase in banded morphs.

Alternative mechanisms for the establishment of this polymorphism include drift and founder effects. Camin and Ehrlich (1958) dismiss these because of the large size of island water snake populations and because all island populations differ from mainland populations in the same way. Though neutral arguments incorporating these observations are conceivable (e.g., temporal bottlenecks in population size, or a single island origin for all island populations), electrophoretic data provide no evidence that such random processes are important (King, 1985).

It is also possible that sexual selection has played a role in the origin and maintenance of this polymorphism. A mating advantage to unbanded males could counter migration of banded morphs from the mainland. Alternatively, a mating advantage to banded males could counter selection for crypsis favoring unbanded morphs. However, there is no evidence that color pattern influences either male-male competition or female choice in water snakes.

The apparent influence of population size on the relative importance of selection and migration suggests several predictions about the future of this polymorphism. On islands where water snake population sizes continue to decrease, banded morphs are expected to increase. However, on islands where population sizes increase, the effect of migration should decrease to the point where selection again becomes apparent and the unbanded morph should increase.

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APPENDIX

Using the method of log-linear models, logarithms of expected values for each cell in the classification table are calculated from a linear combination of parameters corresponding to main effects and interaction terms. For example, expected frequencies (F_{ij}) in a two-way table might be given by:

$$\ln(F_{ij}) = u + u_{1(i)} + u_{2(j)} + u_{12(ij)}$$

where u represents an overall mean effect, $u_{1(i)}$ and $u_{2(j)}$ represent the main effects of the ith and jth levels of variables 1 and 2, respectively, and $u_{12(ij)}$ represents the interaction between levels i and j of variables 1 and 2 (Everitt, 1977). Such a model is easily extended to account for main effects and interactions of additional variables. Log-linear models are hierarchical; a model including a given higher-order interaction also includes lower-order interactions and main effects among those variables.

Models containing all possible main effects and interactions are said to be saturated and necessarily provide a perfect fit to observed data (Everitt, 1977). The fit obtained by unsaturated models is typically tested using the log-likelihood ratio, *G* (Bishop et al., 1974; Fienberg, 1977). A small value of *G* results when expected and observed cell frequencies are similar and indicates a close fit between model and data. Because *G* is additive, independence between two variables can be tested using the difference in *G* between a model including their interaction and one lacking it. A small difference in *G* results when this interaction contributes little to the overall fit of the models and indicates the variables are independent.

In the analysis here, models were fit using a screening process provided by BMDP-77 program P3F (Dixon and Brown, 1977). Independence among variables was tested by first selecting the most parsimonious model (the simplest model for which the significance of *G* was greater than 0.05) and comparing it with a model differing by the presence or absence of interactions between the variables of interest. Two variables were considered to be independent if the probability of *G* associated with their interaction was greater than 0.05. Because calculation of *G* requires all cell frequencies to be greater than 0, 0.5 was added to all cells.

When testing the significance of a particular two-way interaction, other variables can be pooled provided they are independent of one or both of the variables in that interaction (Bishop et al., 1974; Fienberg, 1977). Pooling in this way increases the number of observations in the remaining cells and, hence, increases statistical power.