

## COLOR-PATTERN VARIATION IN LAKE ERIE WATER SNAKES: PREDICTION AND MEASUREMENT OF NATURAL SELECTION

RICHARD B. KING

Department of Biological Sciences, Northern Illinois University,  
DeKalb, Illinois 60115-2861

*Abstract.*—A classic example of natural selection, that of color-pattern variation in Lake Erie island populations of water snakes, was reexamined to overcome shortcomings resulting from classification of snakes into discrete color-pattern categories and use of cross-sectional data. Four continuously varying color-pattern components (DB, the number of dorsal blotches; LB, the number of lateral blotches; ROWS, the height of lateral blotches measured in scale rows; and VEXT, the extent of ventral pigmentation) were analyzed. Patterns of natural selection were predicted from the relationship between color-pattern scores and independent measures of relative crypsis. Tests for natural selection were carried out using longitudinal data on neonate to juvenile-aged snakes and cross-sectional data on juvenile to adult-aged snakes. As predicted, the form of selection differed between younger and older age classes of snakes: selection resulted in a reduction in DB and LB among neonate and juvenile snakes but had little influence on color-pattern components in older snakes. The correspondence between observed patterns of natural selection and predictions based on the relationship between color-pattern scores and relative crypsis supports the hypothesis that differential predation by visual predators on younger age classes of snakes is the mechanism of selection. Gene flow from mainland populations or the initial lack of an allele necessary for reduced pattern may explain why selection has not resulted in greater differentiation between island and mainland populations.

*Key words.*—Color-pattern variation, crypsis, natural selection, *Nerodia sipedon*, predation, snakes.

Received November 3, 1992. Accepted March 31, 1993.

Interest in natural and sexual selection continues to grow as new methodologies make it possible to study selection in realistically complex situations. Particularly useful have been manipulations to extend the range of phenotypic variation on which selection can act (e.g., Sinervo 1990; Andersson 1992), independent tests of performance aimed at making a priori predictions about selection (e.g., Arnold 1983, 1986), methods of analysis that accommodate multiple episodes of selection on suites of correlated characters (Lande and Arnold 1983; Arnold and Wade 1984a,b; Endler 1986; Wade and Kalisz 1990; Kingsolver and Schemski 1991), and integration of these methods with quantitative genetics to predict evolutionary responses to selection (e.g., Arnold 1988; Brodie 1989, 1992; Lynch 1992). In this paper, I use several of these techniques to further analyze a classic example of selection, that of color-pattern variation in Lake Erie island water snakes (Ford 1975; Hedrick et al. 1976; Stebbins 1977).

Color-pattern variation in island populations of the water snake *Nerodia sipedon* is hypothesized to result from a balance between two processes: (1) natural selection for cryptic coloration favoring unbanded morphs along rocky island shorelines, and (2) gene flow from mainland pop-

ulations in which banded morphs are favored (Camin and Ehrlich 1958; Ehrlich and Camin 1960). However, evidence for natural selection in island populations previously reported by Camin and coworkers (Camin et al. 1954; Camin and Ehrlich 1958; Ehrlich and Camin 1960) was not found in my more recent investigation (King 1987). This led me to ask whether hypothesized differences in crypsis, based on human visual perception (Camin et al. 1954; Camin and Ehrlich 1958; Ehrlich and Camin 1960), were born out by quantitative analysis. By evaluating the match between snake color-pattern patch sizes and island background patch sizes, I found that the relationship between color pattern and crypsis was more complex than previously thought (King 1992). Because color-pattern elements increase in size as snakes grow, the match between color pattern and background is size (age) dependent. As a result, the direction of selection may differ among age classes, favoring unbanded morphs among neonates and patterned morphs among older snakes (King 1992). Successfully characterizing natural selection is likely to require analysis of the separate effects of selection acting on different age classes. Tests for natural selection in Lake Erie water snakes carried out by Camin and coworkers were based on com-

parisons between young snakes (captive-born litters or wild-caught neonates) and adults, and thus overlook the possibility that the form of natural selection changes as snakes age. My own comparison of neonates, juveniles, and adults allowed for changes in the form of natural selection as snakes age and suggests that selection favors unbanded morphs among younger snakes but does not discriminate among morphs in older snakes (King 1992; but see King 1987). (Note: the "juvenile" classification of Camin et al. (1954) is equivalent to "young-of-the-year" of King (1987, 1992) and "neonates" in this paper and consists of snakes 8–10 mo of age.)

One shortcoming of previous analyses is that water snakes were classified into a few discrete color pattern categories. Such categorization ignores continuous variation in color-pattern components and may mask differences among samples (e.g., age classes), which result from natural selection. Another shortcoming is that with the exception of the mass-release experiment in King (1987), analyses have been based on cross-sectional data in which pre- and postselection trait distributions are estimated from samples of different age classes (cohorts) collected more or less simultaneously (this contrasts with longitudinal data in which cohorts are followed throughout an episode of selection). Testing for natural selection using cross-sectional data requires more restrictive assumptions than when using longitudinal data. Specifically, trait distributions in younger and older cohorts are assumed to be unaffected by evolutionary processes other than selection (drift, gene flow), the environment, or ontogeny (Lande and Arnold 1983; Arnold and Wade, 1984a,b). This may be a problem in the analyses of Camin and Ehrlich (1958; Ehrlich and Camin 1960) in which data were collected by different investigators over 8 to 20 or more years and pooled across groups of islands.

Here, I analyze Lake Erie water snake color pattern as a suite of continuously varying components. This allows me to recast predictions about natural selection based on the match between snake morphs and backgrounds (King 1992) in terms of individual color-pattern components and to then test for natural selection using techniques designed for continuously varying characters (Lande and Arnold 1983; Schluter 1988). Included in this analysis are longitudinal data on younger age classes of water snakes, which are free of the potential biases described above.

## MATERIALS AND METHODS

### *Color-Pattern Components*

Lake Erie island water snakes exhibit variation in such color-pattern components as number of dorsal and lateral blotches, size of blotches, contrast between blotch and snake ground color, and pattern and extent of ventral pigmentation (see plates I–III in Conant and Clay 1937; fig. 1 in Camin and Ehrlich 1958; and fig. 2 in King 1987). I selected four variables for analysis: number of dorsal blotches anterior to the cloaca (DB), number of lateral blotches anterior to the cloaca (LB, scored on the left side), height of lateral blotches in scale rows (ROWS, scored at midbody), and extent of the venter anterior to the cloaca that was pigmented (VEXT, scored on an ordinal scale from 0–6). These components were selected because they exhibit a broad range of variation, could be scored quickly in the field, and are the basis of a parallel study of color-pattern inheritance (King 1993).

Variation in color-pattern components is heritable with estimates of  $h^2$  from sib analysis ranging from 0.34–0.79 (King 1993). Color-pattern components are positively correlated with each other; phenotypic correlations range from 0.24–0.55, and genetic correlations range from 0.40–0.82 (King 1993).

In addition to being scored for color pattern, snakes were measured to obtain snout–vent length (SVL), classified by sex, individually marked by clipping ventral scales, and released where captured (King 1986, 1987).

### *Prediction of Natural Selection*

Predictions about natural selection were made by generating "performance functions" based on the relationship between a snake's relative crypsis (from King 1992) and its DB, LB, ROWS, and VEXT scores. Relative crypsis was estimated by measuring the size of patches making up snake and background color patterns along random transects across photographic slides of snakes and of island backgrounds, and comparing snake and background patch-size distributions using a measure based on Euclidean distance (King 1992). This measure assumes that to appear cryptic, animals should resemble a random sample of their backgrounds with respect to patch size and other color-pattern components (Endler 1984; Sweet 1985). Different size classes of snakes were analyzed separately because as snakes grow, the patches making up their color

patterns increase in size and as a result, the match between snakes and backgrounds is size (age) dependent (King 1992). The analysis included 143 individual water snakes belonging to four size-age classes: neonates (< 25 cm SVL,  $N = 59$ ), juveniles (35–45 cm SVL,  $N = 28$ ), small adults (60–70 cm SVL,  $N = 26$ ), and large adults (> 80 cm SVL,  $N = 30$ ). Significance tests of the relationship between relative crypsis and color-pattern scores were based on Spearman rank correlations. Performance functions were generated using nonparametric regressions of relative crypsis on color-pattern scores based on the cubic spline (Schluter 1988). As noted in King (1992), estimates of relative crypsis differ somewhat depending on the resolution with which patch size is measured. The analysis presented here is based on a patch-size interval of 2 mm but differences in performance functions obtained using 1 versus 2 mm intervals are noted.

The utility of measures of relative crypsis in making predictions about natural selection depends on how closely performance functions mirror fitness functions. This in turn depends on how my measure of relative crypsis relates to risk of predation within age classes and on the relative intensity of predation among age classes. If one assumes that fitness is a linear function of relative crypsis within age classes and that the risk of predation is similar among age classes, making specific predictions regarding natural selection is straightforward. However, if the relationship between fitness and relative crypsis is assumed to be more complex (e.g., a curvilinear or step function) or the intensity of predation differs among age classes (which is likely as snakes outgrow some potential predators), predictions are necessarily more approximate.

#### *Measurement of Natural Selection*

I obtained longitudinal data on the relationship between color pattern and survival by holding wild-caught gravid females captive until parturition; scoring, marking, and releasing their neonates; and later sampling the survivors. This mass release experiment included 317 neonates (15 litters) released at a single island site in the fall of 1983 and 54 survivors that were recaptured the following spring and summer (King 1987). It provides a test for natural selection occurring over the first 8 to 10 mo of life.

Unfortunately, because recapture rates decrease with time, this method was not practical

for testing for selection among older snakes. To obtain longitudinal data on neonate to juvenile-aged snakes, I took advantage of the fact that because water snakes are born synchronously, within a given period of data collection (May–June), neonates and juveniles fall into discrete body-size categories: neonates measure less than 27 cm snout–vent length (SVL) and are 8 to 10 mo old; juveniles measure 27 to 42 cm SVL and are 20 to 22 mo old (age classifications based on size-frequency distributions and growth rate; King 1986, unpubl. data). Thus, neonates sampled in one year and juveniles sampled in the following year belong to the same cohort, and their color-pattern scores provide estimates of the pre- and postselection distributions for that cohort. Four longitudinal data sets were collected; three from Pelee Island and one from North Bass Island.

Assigning older snakes to cohorts based on body size is difficult because variation in growth rate obscures size cutoffs distinguishing age groups. To test for natural selection occurring among snakes greater than 43 cm SVL (i.e., older than 20–22 mo), I used cross-sectional data collected over three to five successive field seasons. Snakes were classified into three size categories, the juvenile-age class described above, subadults that measured 43 to 58 cm SVL and were estimated to be 32 to 34 mo of age, and adults that measured more than 58 cm SVL and were estimated to be more than 44 mo of age (approximate age classifications are based on growth rates of known individuals). I use the terms subadults and adults for convenience; because males and females reach maturity at different sizes (about 43 cm SVL for males and 59 cm SVL for females, King 1986), the subadult category includes sexually mature males and sexually immature females. Five cross-sectional data sets were analyzed; two from Pelee Island, one from Middle Bass Island, and two from North Bass Island.

Tests for natural selection center on a simple question: do trait distributions differ in mean or variance before and after an episode of selection? However, statistical tests designed to answer this question are not without problems. One method for analyzing selection on suites of characters involves estimation of selection differentials and selection gradients using regression analysis (Lande and Arnold 1983). Regression has proven useful in characterizing selection, in significance testing, and in separating the effects of direct and correlated selection. However, significance tests

(though not point estimates) based on regression may be biased if error terms are not normally distributed. Additionally, selection gradients may be biased if characters are strongly correlated with each other or if important characters under selection have not been included (Lande and Arnold 1983; Endler 1986; Mitchell-Olds and Shaw 1987). In the present study, fitness was scored dichotomously (see below), and thus error terms are unlikely to be normally distributed; characters were phenotypically and genetically correlated (King 1993); and the likely target of selection, crypsis, may depend partly on unmeasured color-pattern components. In contrast to regression, randomization tests (Jayne and Bennett 1990) and the cubic spline (Schluter 1988) provide methods for significance testing and characterizing selection that make no assumptions about trait or fitness distributions. However, randomization tests require longitudinal data and cubic splines are strictly descriptive. In the present study, tests for selection are further complicated by the presence of multiple data sets to be analyzed. Given these problems, I have used several approaches to characterizing the effects of natural selection.

When testing for differences among means, I used multivariate analysis of variance (MANOVA) to compare color-pattern scores of fitness classes (survivors and nonsurvivors in the mass release experiment; preselection and postselection samples in other data sets). Color-pattern components were treated as a suite of correlated dependent variables and fitness and data set were treated as independent factors.

To provide a description of the form and strength of natural selection, I computed selection differentials and selection gradients using regression (Lande and Arnold 1983). Color-pattern scores were standardized (to mean of 0 and variance of 1), and relative fitness was computed by dividing fitness by mean fitness (nonsurvivors in the mass release experiment and members of preselection samples in other data sets were assigned a fitness of 0; survivors in the mass release experiment and members of postselection samples in other data sets were assigned a fitness of 1). Standardized selection differentials, which describe the combined effects of direct and correlated selection, were estimated by the regression coefficients from separate regressions of relative fitness on each standardized color-pattern component (directional-selection differentials) and on the square of each color-pattern com-

ponent (quadratic-selection differentials). Standardized selection gradients, which describe the effects of direct selection alone, were estimated by the partial regression coefficients from multiple regression of relative fitness on all four color-pattern components (directional-selection gradients) and by the partial regression coefficients of squared terms from multiple regression of relative fitness on the four color-pattern components, squares of the four color-pattern components, and cross products of the six pairwise combinations of components (quadratic selection gradients). Correlational selection gradients were generally small and variable in sign among samples for a given age class, and are thus not presented.

I present a graphical representation of the effects of natural selection using fitness functions generated using nonparametric regression based on the cubic spline (Schluter 1988).

The use of regression to estimate selection differentials and gradients and cubic splines to generate fitness functions is best suited to longitudinal data (e.g., the mass release experiment and the neonate-juvenile data sets in this study). For this reason, selection differentials, selection gradients, and fitness functions based on cross-sectional data for juvenile to adult-aged snakes are necessarily approximate.

#### *Assumptions*

In addition to statistical assumptions described above, three further assumptions were made.

*Ontogenetic Stability of Color Pattern Scores.*— One assumption was that color pattern scores did not change as snakes age. Pattern elements remain fixed in position and size over the life of a water snake (Conant 1951; Beatson 1976; King 1987); but pattern elements sometimes fade as snakes age, resulting in a decrease in the contrast between blotches and ground color. Though care was taken to accurately score color-pattern components in the field (e.g., by immersing snakes prior to scoring color pattern), differences in how snakes belonging to different age classes were scored could influence the outcome of tests for natural selection. To test for constancy in my scoring of color pattern, I analyzed color-pattern scores of individuals that had been caught and scored for color pattern multiple times. Specifically, I tested whether differences in color-pattern scores were correlated with time elapsed between captures, initial SVL, or change in SVL

between captures. Ninety snakes ranging from 19 cm to 100 cm SVL (mean = 69.9 cm) were recaptured 6 to 2552 d (mean = 562.8 d) after initial capture. Using an experimentwise alpha of 0.05 (and a testwise alpha of  $0.05/12 = 0.004$ ), difference in DB, LB, ROWS, and VEXT were all uncorrelated with time elapsed between captures ( $r = -0.11$ – $0.17$ ), initial SVL ( $r = -0.20$ – $0.11$ ), and change in SVL between captures ( $r = -0.11$ – $0.27$ ). Using a testwise alpha of 0.05, only one correlation was significant: difference in VEXT was positively correlated with change in SVL between captures ( $r = 0.27$ ,  $P = 0.01$ ).

*Independence of Color Pattern and Capture Probability.*—Another assumption was that my ability to capture snakes was unbiased with respect to color pattern. I tested this assumption by comparing scores of snakes that were visible (basking or in motion) prior to capture with those that were hidden (captured from under cover of objects). My reasoning was that because detecting hidden snakes requires visually scanning a relatively small area from a short distance, capture success of hidden snakes should not be affected by color pattern. Analysis was restricted to subadults and adults because younger snakes were rarely captured while visible (< 10% of neonates and juveniles were visible whereas > 50% of subadults and adults were visible). MANOVA was used to compare color-pattern scores of visible and hidden snakes with sample included as an independent factor. Although there was no significant main effect of status (visible or hidden) (Pillai's trace < 0.01; approximate  $F = 0.19$ ;  $df = 4$ , 547;  $P < 0.944$ ), there was a significant status-by-sample interaction (Pillai's trace = 0.07; approximate  $F = 1.76$ ;  $df = 24$ , 2200;  $P = 0.014$ ). Univariate analyses indicated that this interaction could be attributed to variation in VEXT ( $F = 2.75$ ,  $P = 0.012$ ) and not in DB ( $F = 0.96$ ,  $P = 0.449$ ), LB ( $F = 0.44$ ,  $P = 0.850$ ), or ROWS ( $F = 0.97$ ,  $P = 0.448$ ).

*Similarity of Males and Females.*—A final assumption was that males and females did not differ in color pattern. This was an assumption of convenience rather than necessity; it increased sample size by allowing inclusion of snakes, especially neonates, which were not classified by sex. I compared color-pattern scores of males and females using MANOVA with age (juvenile, subadult, adult) and sample as independent factors. MANOVA revealed a significant main effect of sex (Pillai's trace = 0.02; approximate  $F = 4.89$ ;  $df = 4$ , 882;  $P = 0.001$ ). Univariate anal-

ysis revealed that this could be attributed to variation in VEXT ( $F = 10.44$ ,  $P = 0.001$ ) and not in DB ( $F = 0.12$ ,  $P = 0.73$ ), LB ( $F = 2.98$ ,  $P = 0.09$ ), or ROWS ( $F = 1.44$ ,  $P = 0.23$ ). Overall, VEXT scores of males exceeded those of females by a mean of 0.34 (VEXT ranged from 0–6).

These analyses suggest that assumptions of ontogenetic stability, independence of color pattern and capture probability, and similarity of males and females were generally met. Exceptions all involve the color-pattern component VEXT, which may increase ontogenetically, may not be independent of capture probability (a surprising result given that VEXT was not visible in either active or inactive snakes), and is somewhat greater in males than in females. Given these results, conclusions regarding the effect of selection on VEXT are tentative.

#### *Statistical Software*

Cubic splines were generated using the program described by Schluter (1988); all other analyses were carried out using SPSS-PC version 3.2 (Norusis 1988a,b).

## RESULTS

### *Prediction of Natural Selection*

Relative crypsis was negatively correlated with all four color-pattern components among neonates and positively correlated with all four color-pattern components in the three older age classes of snakes (table 1). Except for VEXT among juveniles, these correlations were all significantly different from 0 (table 1). This pattern is reflected in performance functions relating relative crypsis and color-pattern scores (fig. 1). Relative crypsis decreased with increasing color-pattern score for neonates but increased with increasing color-pattern score for the three older age classes of snakes. Performance functions based on relative crypsis estimates using a patch-size interval of 1 mm differed only in that relative crypsis decreased less steeply with increasing color-pattern score among neonates (data not shown).

These results suggest the following predictions about the occurrence of natural selection: (1) The form of natural selection differs between younger and older age classes of snakes. (2) Relative fitness of snakes with low color-pattern scores is greater among younger snakes than among older snakes. (This prediction could be borne out in several ways: for example, if fitness decreases with increasing color-pattern score among young

TABLE 1. Spearman rank correlations between color-pattern scores and relative crypsis against island backgrounds for four size-age classes of Lake Erie water snakes. Two-tailed probabilities are shown in parentheses.

	<i>N</i>	DB	LB	ROWS	VEXT
Neonates (< 25 cm SVL)	59	-0.41 (0.002)	-0.40 (0.002)	-0.28 (0.029)	-0.29 (0.025)
Juveniles (35-45 cm SVL)	28	0.66 (< 0.001)	0.64 (< 0.001)	0.67 (< 0.001)	0.13 (0.512)
Small adults (60-70 cm SVL)	26	0.71 (< 0.001)	0.56 (0.004)	0.71 (< 0.001)	0.43 (0.027)
Large adults (> 80 cm SVL)	30	0.66 (< 0.001)	0.56 (0.002)	0.71 (< 0.001)	0.50 (0.005)

snakes but remains unchanged with increasing color-pattern score among older snakes; if fitness increases with increasing color-pattern score among snakes of all age classes but increases more steeply in older snakes.) (3) Selection is primarily directional; strong stabilizing and disruptive selection is lacking. (4A) Selection favors decreased color-pattern scores among younger snakes; (4B) Selection favors increased color-pattern scores among older snakes (a specific form of prediction 2). (5) The shift in the form of selection occurs between 25 cm and 35 cm SVL. (6) Because es-

timates of relative crypsis were based on lateral and dorsal (but not ventral) components of color-pattern, performance functions for VEXT represent expected correlated responses to selection on other color-pattern components and predict that VEXT should decrease among young snakes and increase among older snakes.

#### Measurement of Natural Selection

Color-pattern scores of preselection and post-selection samples of water snakes are summarized in table 2. A test for selection acting on

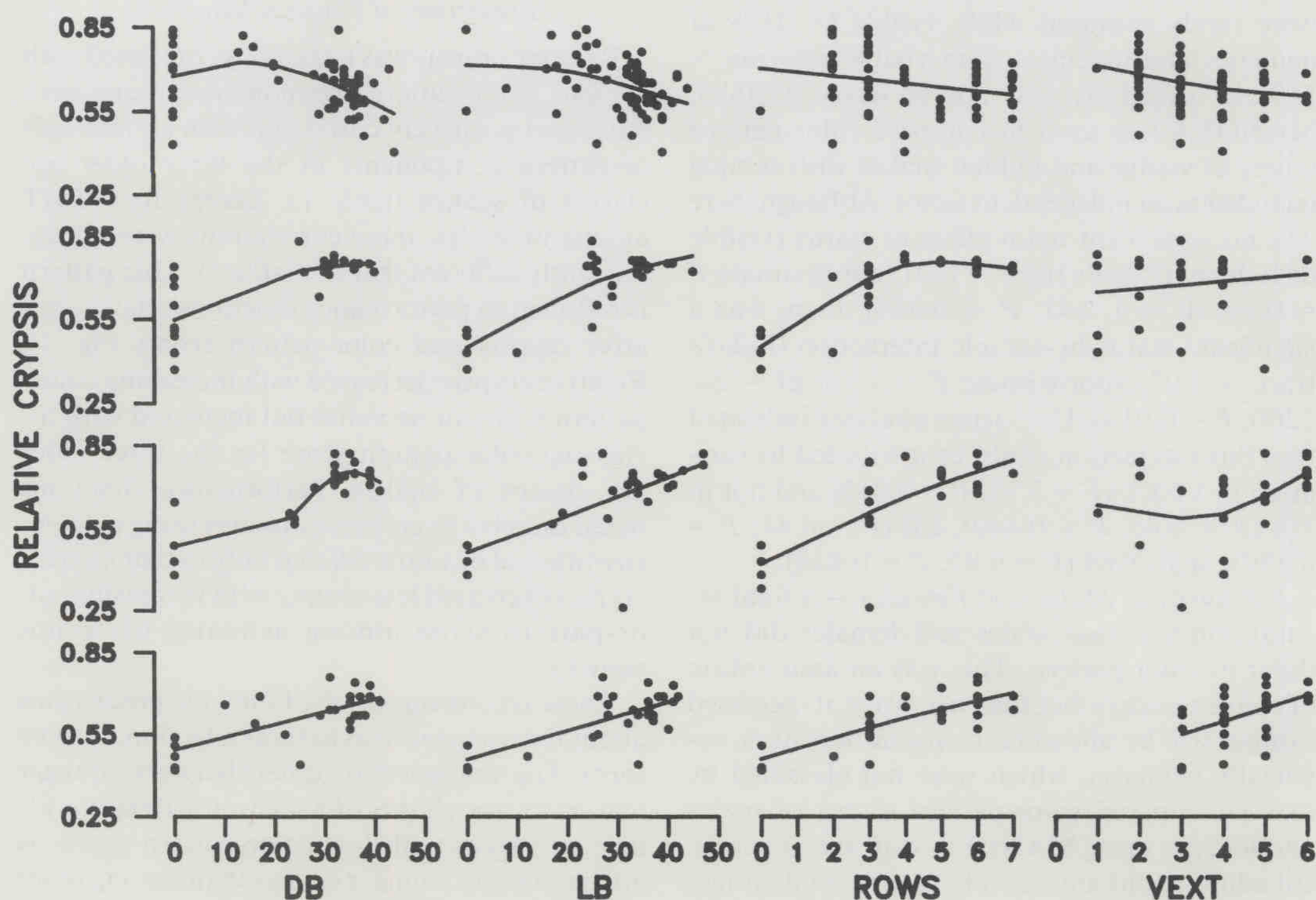


FIG. 1. Performance functions of Lake Erie water snake color-pattern components based on the cubic spline for neonates (top row), juveniles (second row), small adults (third row), and large adults (fourth row). Each point represents an individual snake.

TABLE 2. Means (standard deviations) of color-pattern scores for samples of Lake Erie water snakes used to test for natural selection among (A) neonates, (B) neonate to juvenile-aged snakes, (C) juvenile, subadult, and adult-aged snakes.

	<i>N</i>	DB	LB	ROWS	VEXT
A. Mass-release experiment					
Recaptured	54	32.9 (11.80)	33.5 (4.43)	4.2 (1.43)	4.2 (1.27)
Not recaptured	263	36.1 (6.50)	34.9 (4.63)	4.3 (1.45)	4.2 (1.58)
B. Longitudinal samples of wild-caught snakes					
Pelee Island					
Neonates, 1982	17	35.5 (2.88)	35.5 (3.97)	5.8 (1.35)	4.2 (1.13)
Juveniles, 1983	19	33.0 (4.45)	35.9 (3.61)	6.0 (0.88)	5.1 (1.10)
Neonates, 1989	44	33.2 (6.43)	36.4 (4.35)	5.0 (1.09)	4.1 (1.29)
Juveniles, 1990	24	26.5 (12.92)	31.0 (6.29)	4.8 (1.42)	4.3 (1.19)
Neonates, 1990	35	34.5 (4.52)	36.3 (5.36)	5.3 (1.06)	4.1 (1.16)
Juveniles, 1991	22	32.5 (8.35)	31.3 (7.64)	5.0 (1.70)	4.1 (1.08)
North Bass Island					
Neonates, 1989	15	31.3 (13.57)	33.8 (8.11)	3.7 (1.23)	4.3 (1.10)
Juveniles, 1990	12	27.9 (17.01)	27.8 (9.50)	3.6 (1.44)	4.4 (1.62)
C. Cross-sectional samples of wild-caught snakes					
Pelee Island, 1981-1985					
Juveniles	44	29.7 (11.36)	32.7 (8.63)	5.3 (1.61)	4.6 (1.44)
Subadults	60	29.2 (9.97)	29.9 (6.44)	4.9 (1.48)	4.4 (1.40)
Adults	107	30.4 (13.49)	31.9 (6.40)	4.3 (1.33)	4.6 (1.16)
Pelee Island, 1989-1991					
Juveniles	67	30.1 (11.29)	31.8 (7.87)	4.7 (1.61)	4.2 (1.22)
Subadults	66	27.6 (14.31)	28.2 (9.85)	4.2 (1.74)	4.1 (0.99)
Adults	105	27.7 (11.80)	31.4 (7.25)	4.9 (1.48)	4.5 (1.05)
Middle Bass Island, 1981-1984					
Juveniles	27	31.4 (12.32)	31.6 (8.35)	4.3 (1.66)	4.0 (1.34)
Subadults	24	30.4 (12.30)	29.4 (9.86)	4.0 (1.68)	4.3 (1.40)
Adults	73	28.0 (12.54)	27.5 (11.29)	4.1 (2.02)	4.6 (1.36)
North Bass Island, 1981-1984					
Juveniles	24	25.4 (16.87)	33.0 (5.08)	4.3 (1.75)	3.9 (1.06)
Subadults	31	29.6 (11.36)	28.6 (8.54)	3.8 (1.29)	4.5 (1.09)
Adults	113	25.9 (13.36)	29.0 (9.65)	4.0 (1.75)	4.4 (1.21)
North Bass Island, 1988-1991					
Juveniles	16	28.7 (15.25)	28.1 (9.13)	3.7 (1.40)	4.4 (1.50)
Subadults	27	30.4 (13.49)	31.9 (6.40)	4.3 (1.33)	4.6 (1.16)
Adults	79	28.6 (13.70)	29.1 (10.57)	3.9 (1.56)	4.4 (1.05)

neonates using MANOVA of data from the mass-release experiment was statistically significant (table 3A). These results are reflected in the large negative directional selection differentials for DB and LB (table 4A). In addition, a positive quadratic selection differential for DB and a negative quadratic selection differential for VEXT were present (table 4A). Selection gradients differ from selection differentials only in that they suggest additionally that directional selection favors increased VEXT (table 4A).

A test for selection acting on neonate- to juvenile-aged snakes using MANOVA was statistically significant (table 3B). Across the four data

sets, directional selection differentials were generally negative and of moderate magnitude for both DB and LB (table 4B). Directional selection differentials for ROWS and VEXT and quadratic selection differentials for all four color-pattern components were mostly small and varied in sign among samples (table 4B). Selection gradients indicate that either DB or LB were consistently the target of negative directional selection (table 4B).

A test for selection acting on juvenile to subadult-aged snakes using a MANOVA approached statistical significance ( $P = 0.052$ ) (table 3C). Selection differentials and gradients were

TABLE 3. Significance of fitness main effects and sample  $\times$  fitness interactions from MANOVA of color-pattern scores from preselection and postselection samples for (A) neonates in the mass-release experiment, (B) neonate to juvenile-aged snakes, (C) juvenile to subadult-aged snakes, and (D) subadult to adult-aged snakes.

	Pillai's Trace	F	df	P
A. Mass-release experiment				
Fitness	0.03	2.65	4, 312	0.033*
B. Neonate to juvenile-aged snakes				
Sample $\times$ fitness	0.07	1.02	12, 537	0.430
Fitness	0.14	7.24	4, 177	0.001***
C. Juvenile to subadult-aged snakes				
Sample $\times$ fitness	0.05	1.22	16, 1504	0.248
Fitness	0.02	2.37	4, 373	0.052
D. Subadult to adult-aged snakes				
Sample $\times$ fitness	0.03	1.44	16, 2700	0.113
Fitness	0.01	2.17	4, 672	0.071

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .

generally small and variable in sign for all components except LB, for which they were negative in four of the five samples (table 4C).

A test for selection acting on subadult to adult-aged snakes using MANOVA approached statistical significance ( $P = 0.071$ ) (table 3D). However, selection differentials and gradients were generally small and variable in sign (table 4D).

Fitness functions based on the cubic spline corroborate these results (fig. 2). Among neonate and juvenile-aged snakes, fitness functions decrease with increasing DB and LB but showed no consistent form for ROWS or VEXT. Among older snakes, fitness functions showed no consistent form for any color-pattern component. Fitness functions for DB and VEXT from the mass-release experiment were curvilinear (fig. 2), consistent with the quadratic selection gradients reported above for these components. No local fitness minimum existed for DB, as would be expected if disruptive selection were operating. However, there was a local fitness maximum for VEXT, suggesting that stabilizing selection influenced this component.

#### DISCUSSION

*The Occurrence of Natural Selection.* — The results presented here support the hypothesis that natural selection favors less patterned water snakes in island populations (Camin et al. 1954; Camin and Ehrlich 1958; Ehrlich and Camin 1960). However, the present analysis goes beyond previous studies in several important ways. By providing an independent measure of the match between snakes and backgrounds, it pro-

vides strong evidence that differential predation by visual predators is the likely mechanism of selection. Furthermore, by testing for selection on specific age classes of snakes, the present analysis makes clear that it is neonate to juvenile-aged snakes that are most subject to selection. This conclusion is strengthened by the fact that evidence for selection in these age classes is based on longitudinal data and thus is free of biases that may have affected previous analyses based on cross-sectional data.

The results presented here contrast with my previous analysis in which no evidence of natural selection was found (King 1987). Part of this difference appears to be caused by increased sensitivity to natural selection gained by treating color pattern as a continuous rather than categorical variable. This is apparent in the mass-release experiment that provided no evidence for selection when morphs were scored as banded, intermediate, or unbanded (King 1987) but provides evidence of selection for reduced color pattern in the present analysis.

Despite general agreement with the results of Camin and coworkers, the results presented here do not suggest selection is as strong as hypothesized by Camin and Ehrlich (1958; Ehrlich and Camin 1960). Those authors note that "if we divide the pattern spectrum into only two classes, the young snakes in the heavily banded half of the litter population have a chance of survival which is only about 23% that enjoyed by those in the relatively unbanded half" (Ehrlich and Camin 1960, p. 136). In contrast, if snakes in my mass release experiment are divided into two



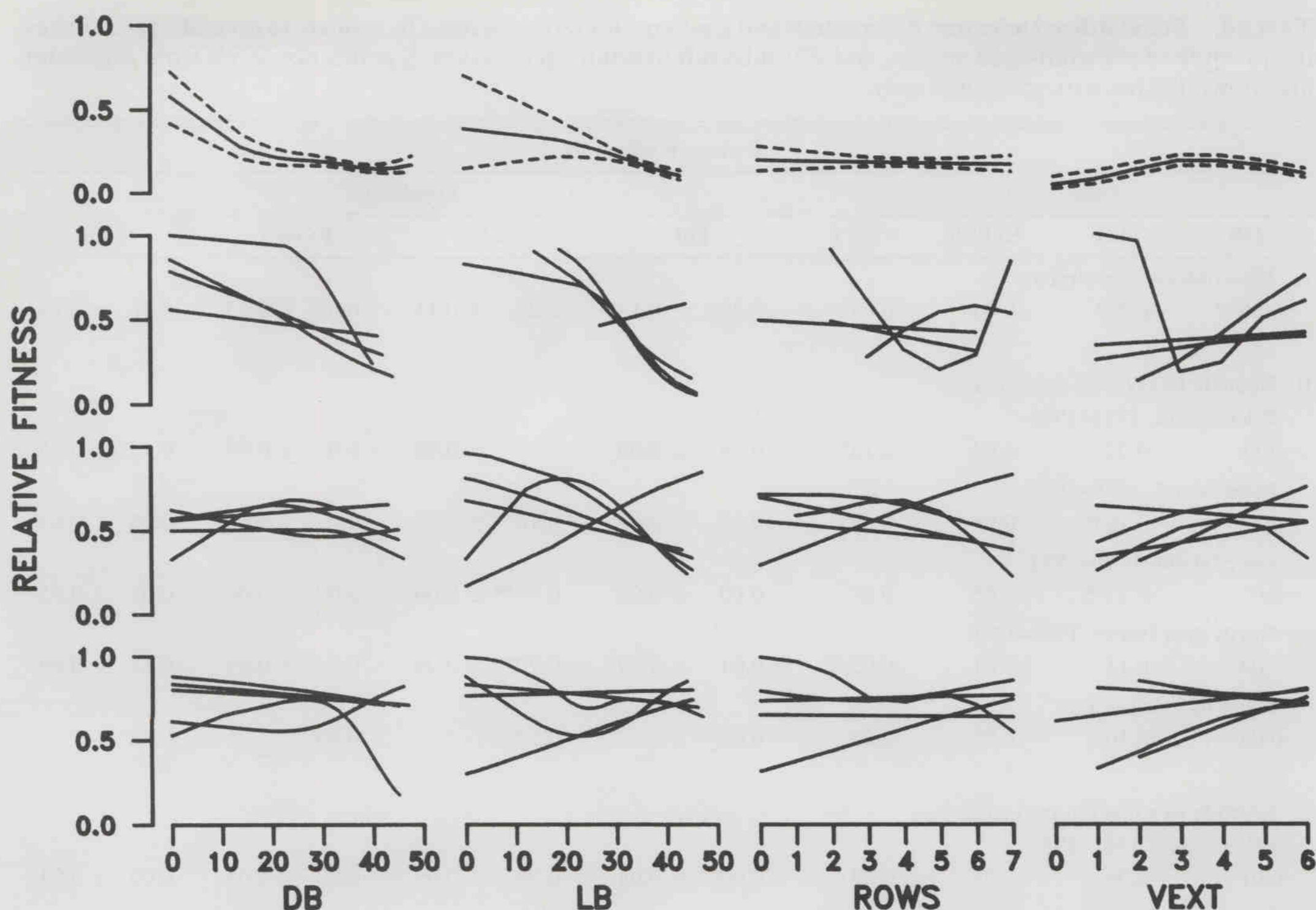


FIG. 2. Fitness functions of Lake Erie water snake color-pattern components based on the cubic spline for neonates (top row), neonate to juvenile aged snakes (second row), juvenile to subadult aged snakes (third row), and subadult to adult aged snakes. For neonates, dashed lines show  $\pm 1$  SE. For older snakes, each line represents a different sample; SE's were omitted for clarity.

equal groups based on DB or LB, apparent survival of the more patterned group is about 60% that of the less patterned group.

Results of tests for natural selection presented here are consistent with many of the predictions generated by my analysis of the relationship between color-pattern score and relative crypsis. Consistent with prediction 1, the form of natural selection differs between younger and older snakes: selection on young snakes is evident, whereas selection on older snakes appears absent. Consistent with prediction 2, relative fitness of snakes with low scores for DB and LB is greater among younger snakes than among older snakes. Consistent with prediction 3, the strongest components of selection appear to be directional. Moderate quadratic selection differentials and gradients are sometimes present (table 4), but except for VEXT in the mass-release experiment, fitness functions do not show consistent maxima or minima (fig. 2). Consistent with prediction 4A, selection favors a decrease in DB and LB among younger snakes. In general agreement

with prediction 5, the shift in the form of natural selection occurs between 27 and 43 cm SVL. Fitness functions of neonates (<27 cm SVL) and of neonate to juvenile-aged (27 cm–43 cm SVL) snakes are similar to each other but differ from fitness functions of juvenile to subadult-aged (43 cm–58 cm SVL) snakes.

Contrary to prediction 4B, selection does not appear to favor more patterned individuals among older snakes. However, this is not entirely unexpected. Adult water snakes can attain a length of more than a meter and a mass of more than 500 g (King 1986). This, together with their generally aggressive demeanor (pers. obs.), suggests that larger water snakes may prove difficult for many predators to subdue and are at low risk of predation regardless of how well they match their background.

Contrary to prediction 6, VEXT appears to be a direct target of directional and stabilizing selection rather than changing only in response to selection on correlated characters. However, sexual differences and ontogenetic changes poten-

TABLE 4. Standardized selection differentials and gradients for (A) neonates, (B) neonate to juvenile-aged snakes, (C) juvenile to subadult-aged snakes, and (D) subadult to adult-aged snakes. Significance levels from regression are shown for heuristic purposes only.

				Direction selection			
Differentials				Gradients			
DB	LB	ROWS	VEXT	DB	LB	ROWS	VEXT
<b>A. Mass-release experiment</b>							
-0.35**	-0.25*	-0.03	-0.03	-0.30* ± 0.13	-0.27 ± 0.15	0.01 ± 0.15	0.16 ± 0.14
<b>B. Neonate to juvenile-aged snakes</b>							
Pelee Island, 1982-1983							
-0.11	0.02	0.04	0.13*	-0.14 ± 0.06	0.07 ± 0.06	-0.02 ± 0.05	0.12* ± 0.05
Pelee Island, 1989-1990							
-0.12**	-0.16***	-0.04	0.02	-0.05 ± 0.05	-0.16* ± 0.05	0.03 ± 0.04	0.05 ± 0.04
Pelee Island, 1990-1991							
-0.05	-0.13**	-0.05	0.01	0.03 ± 0.05	-0.19** ± 0.06	0.07 ± 0.06	0.01 ± 0.05
North Bass Island, 1989-1990							
-0.04	-0.12	-0.01	0.02	-0.01 ± 0.09	-0.20* ± 0.09	0.04 ± 0.09	0.12 ± 0.09
Mean of four samples							
-0.08	-0.10	-0.02	0.05	-0.04	-0.12	0.03	0.08
<b>C. Juvenile to subadult-aged snakes</b>							
Pelee Island, 1981-1985							
-0.01	-0.06	-0.05	-0.02	0.07 ± 0.04	-0.08 ± 0.05	-0.03 ± 0.05	0.00 ± 0.03
Pelee Island, 1989-1991							
-0.03	-0.07*	-0.05	-0.02	0.02 ± 0.04	-0.07 ± 0.05	-0.01 ± 0.04	-0.01 ± 0.03
Middle Bass Island, 1981-1984							
-0.02	-0.04	-0.02	0.04	0.02 ± 0.07	-0.07 ± 0.08	-0.01 ± 0.07	0.06 ± 0.05
North Bass Island, 1981-1984							
0.05	-0.09*	-0.04	0.08	0.13** ± 0.05	-0.14** ± 0.05	-0.04 ± 0.05	0.05 ± 0.04
North Bass Island, 1988-1991							
0.02	0.07	0.07	0.02	-0.02 ± 0.06	0.06 ± 0.07	0.03 ± 0.07	-0.01 ± 0.06
Mean of five samples							
0.00	-0.04	-0.02	0.02	0.04	-0.06	-0.01	0.02
<b>D. Subadult to adult-aged snakes</b>							
Pelee Island, 1981-1985							
0.01	0.01	0.00	0.03*	0.01 ± 0.02	0.02 ± 0.02	-0.03 ± 0.02	0.03* ± 0.01
Pelee Island, 1989-1991							
0.00	0.03*	0.04**	0.04**	-0.05** ± 0.02	0.02 ± 0.02	0.05* ± 0.02	0.03* ± 0.01
Middle Bass Island, 1981-1984							
-0.01	-0.01	0.00	0.01	-0.01 ± 0.02	-0.04 ± 0.03	0.03 ± 0.03	0.02 ± 0.02
North Bass Island, 1981-1984							
-0.02	0.00	0.01	0.00	-0.04* ± 0.02	0.02 ± 0.02	0.01 ± 0.02	0.00 ± 0.01
North Bass Island, 1988-1991							
-0.01	-0.02	-0.02	-0.01	0.01 ± 0.02	-0.02 ± 0.03	-0.01 ± 0.02	0.00 ± 0.02
Mean of five samples							
-0.01	0.00	0.01	0.01	-0.02	0.00	0.01	0.02

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

tially confound conclusions regarding selection on VEXT (see Assumptions).

Estimates of selection gradients assume all significant targets of selection are included (Lande

and Arnold 1983; Endler 1986; Mitchell-Olds and Shaw 1987). As noted earlier, unmeasured color-pattern components may contribute to crypsis. For example, selection may favor re-

TABLE 4. Extended.

Quadratic selection							
Differentials				Gradients			
DB	LB	ROWS	VEXT	DB	LB	ROWS	VEXT
0.12***	0.00	-0.03	-0.27*	0.14* ± 0.07	-0.04 ± 0.10	-0.05 ± 0.18	-0.35* ± 0.16
0.04	-0.02	-0.05	-0.01	0.15 ± 0.09	0.12 ± 0.10	0.02 ± 0.09	0.10 ± 0.07
0.04*	0.07*	0.07	-0.03	0.05 ± 0.06	0.05 ± 0.04	0.01 ± 0.06	-0.02 ± 0.04
0.01	0.06	0.11**	-0.02	0.00 ± 0.03	0.14 ± 0.09	0.20* ± 0.08	-0.01 ± 0.03
0.03	0.01	0.02	0.08	0.07 ± 0.13	-0.11 ± 0.21	-0.07 ± 0.12	0.24 ± 0.13
0.03	0.03	0.04	0.01	0.07	0.05	0.04	0.08
-0.01	-0.01	-0.01	-0.01	0.03 ± 0.06	-0.06 ± 0.07	0.00 ± 0.06	0.04 ± 0.04
0.03	0.02	0.02	-0.04	0.02 ± 0.05	-0.02 ± 0.06	-0.09 ± 0.07	-0.05* ± 0.03
0.00	0.01	0.00	0.01	-0.01 ± 0.09	-0.18 ± 0.16	-0.32 ± 0.19	-0.04 ± 0.06
-0.06*	0.02	-0.10*	0.01	-0.15 ± 0.08	0.06 ± 0.06	-0.08 ± 0.07	-0.04 ± 0.05
-0.01	-0.02	-0.01	-0.04	0.11 ± 0.17	-0.05 ± 0.12	-0.01 ± 0.16	-0.02 ± 0.07
-0.01	0.00	-0.02	-0.01	0.00	-0.05	-0.10	-0.02
0.00	0.01	0.00	-0.04**	0.02 ± 0.02	0.02 ± 0.03	-0.05 ± 0.03	-0.04** ± 0.01
-0.01	-0.01	-0.02	-0.01	-0.04 ± 0.02	-0.04 ± 0.03	-0.02 ± 0.04	0.01 ± 0.01
0.00	0.01	0.02	0.00	-0.02 ± 0.02	0.02 ± 0.06	0.07 ± 0.05	0.01 ± 0.02
0.01	0.00	0.02	0.01	0.01 ± 0.02	-0.04 ± 0.03	-0.02 ± 0.03	0.00 ± 0.01
0.00	0.01	0.01	-0.01	-0.03 ± 0.03	0.00 ± 0.04	0.01 ± 0.04	-0.01 ± 0.01
0.00	0.00	0.01	-0.01	-0.01	-0.01	0.00	-0.01

duced contrast between color-pattern elements against island backgrounds and reduced DB and LB could represent correlated responses to such selection. Reflectance measurements of snakes

and backgrounds (e.g., King and King 1991) would provide a means of assessing whether selection on such color-pattern components is likely. Estimates of selection gradients are also af-

ected by correlations among traits (Lande and Arnold 1983; Endler 1986; Mitchell-Olds and Shaw 1987). As noted earlier, color-pattern components are phenotypically and genetically correlated with the strongest correlation being between DB and LB (phenotypic correlation = 0.55, genetic correlation = 0.82, King 1993). However, excluding DB from calculations of selection gradients has little effect on the conclusions presented here (data not shown).

*Mechanism of Natural Selection.*—The correspondence between observed patterns of selection and predictions based on the relationship between color-pattern score and relative crypsis lends credence to the hypothesis that differential predation by visual predators is the mechanism of selection. However, direct evidence supporting this hypothesis is lacking. Birds, particularly gulls, herons, and raptors, are thought to be important snake predators in the Lake Erie area (Camin and Ehrlich 1958; King 1987) (for documentation that these birds feed on snakes see Guthrie 1932; Floyd 1933; Kushlan 1978). Crows, robins, and jays are also present in the island region and are important predators on snakes elsewhere (Aleksiuk 1977; Jayne and Bennett 1990; Brodie 1992). However, observations of avian predation on snakes in the island region are limited to a gull (Goldman 1971), a heron (Hoffman and Curnow 1979), and a robin (*Turdus migratorius*) (pers. obs.). It is also possible that predatory fish attack water snakes while they are foraging in Lake Erie. Several species of fish prey on water snakes (Brown 1940; McGrew 1963; Black 1983), and the Lake Erie fish fauna includes species capable of subduing small to moderate sized water snakes. However, differences between island and mainland aquatic backgrounds parallel differences in terrestrial backgrounds (exposed limestone and dolomite versus vegetated soil, clay, and sand), thus selection generated by aquatic predators may be similar to that expected from terrestrial predators. Identifying important predators could aid in evaluating the viewing conditions and predator visual characteristics for which snake color patterns need to appear cryptic (e.g., Endler 1991).

My analysis of relative crypsis assumes that water snake color patterns function to reduce detection by visual predators while snakes are stationary (King 1992). Alternatively, color patterns may function to generate illusions of motionlessness or reduced velocity while snakes are

moving or provide crypsis when snakes suddenly cease motion (Jackson et al. 1976; Pough 1976; Brodie 1989, 1992). These alternative functions are suggested by correlations between escape behavior and color pattern within and among species (Brodie 1989; Jackson et al. 1976): banded and regularly blotched snakes tend to remain motionless or reverse direction and freeze during flight, whereas striped and uniform snakes tend to exhibit straight-line flight. In an elegant study of escape behavior and color pattern in the garter snake *Thamnophis ordinoides*, Brodie has recently demonstrated that such correlations are genetically based (Brodie 1989) and can themselves be the target of natural selection (Brodie 1992). The possibility that differences in escape behavior among differently patterned Lake Erie water snakes acts to ameliorate differences in crypsis of stationary snakes deserves investigation.

The contribution of snake color patterns to illusions of motionlessness and reduced velocity also deserves further study. Empirical evidence for such illusions comes mostly from studies of pattern perception in humans (e.g., Brown 1931a,b), and though many characteristics of human visual systems may apply to nonhuman vertebrates (Kiltie and Laine 1992), studies of the interaction between color pattern and escape behavior that take into account visual abilities of important predators are needed. Experiments using moving prey models and live predators (e.g., Kiltie 1992) provide one useful approach to this problem.

Another way that behavior may ameliorate selective differences among water snakes differing in color pattern is through microhabitat selection (King 1992). Because crypsis is background dependent (Endler 1978, 1984, 1991), morph-specific background choice could reduce differences in crypsis and hence the effects of natural selection. Although differences in background use by Lake Erie water snakes are not apparent from incidental observations of free-ranging snakes (pers. obs.), direct tests have not been conducted.

*Evolutionary Responses to Selection.*—It is tempting to combine selection gradients reported here with estimates of heritability and genetic correlation (King 1993) to predict evolutionary responses of color-pattern components in island water snake populations. However, because selection gradients and heritability estimates have rather large standard errors, predicted responses

to selection would be approximate at best. In addition, selection gradients are based on the preselection distribution of color-pattern scores *at the onset of that episode*, and thus do not strictly sum to lifetime selection gradients (Arnold and Wade 1984a,b). Finally, because of imperfect age classification, episodes of selection analyzed here may overlap.

What is clear is that given the significant heritability and positive phenotypic and genetic correlations of color-pattern components (King 1993) and the fact that the strongest components of selection are for reduced DB and LB, the expected evolutionary response is an overall reduction in color pattern. In fact, if color-pattern components are treated singly, observed heritabilities (King 1993) and selection gradients (table 4) could produce a reduction in DB and LB of more than 0.1 standard deviation each generation. Given that island populations have been isolated for somewhat more than 1000 generations (about 4000 yr, King 1987), evolutionary responses of this magnitude would be expected to have produced even greater differentiation than is observed between island and mainland populations.

At least two factors may explain why greater differentiation has not occurred. One factor is gene flow from mainland populations that consist almost entirely of regularly patterned individuals (Conant and Clay 1937; pers. obs.). To determine whether gene flow might reasonably be expected to balance observed levels of selection in island populations, R. Lawson and I are estimating rates of gene flow from patterns of allozyme variation within and among island and mainland water snake populations.

Another factor that may have slowed differentiation between island and mainland water snake populations relates to the genetic basis of color-pattern variation. Elsewhere, I have suggested that reduced color pattern in island water snake populations is controlled in part by a recessive allele at a major locus: homozygotes for this recessive allele have reduced pattern, heterozygotes and homozygotes for the dominant allele are regularly patterned (King 1993). With such a mode of inheritance, heritability and genetic correlations will change from generation to generation as allele frequencies at this major locus change and long-term prediction of evolutionary responses will likely be misleading. For example, if the recessive allele was initially rare

in island populations, there would have been little variation in color pattern on which selection could act. Only as the recessive allele increased in frequency might evolutionary responses approach the magnitude suggested above. The apparently subdivided population structure of Lake Erie water snake populations suggests a possible role for genetic drift during the initial stages of population differentiation, as in Wright's shifting balance (Wright 1931, 1988). Natural selection may not have become important until some time after island populations became isolated and levels of phenotypic and genetic variation in color pattern increased. Camin and Ehrlich (1958) dismissed drift as a factor in the *maintenance* of color-pattern variation in island water snakes populations. However, it remains plausible that drift played a role during the initial stages of differentiation between island and mainland populations.

#### ACKNOWLEDGMENTS

The work described here was carried out under permits from the Ontario Ministry of Natural Resources and the Ohio Department of Natural Resources, with approval from the Indiana University Bloomington Animal Resource Center and the Northern Illinois University Institutional Animal Care and Use Committee, and financial support from Sigma Xi, the American Museum of Natural History, the Society for the Study of Amphibians and Reptiles, the American Society of Ichthyologists and Herpetologists, a Purdue University David Ross Fellowship, the Ohio Department of Natural Resources, the Ontario Ministry of Natural Resources, and (during manuscript preparation) the National Science Foundation (BSR-9107382 to R. King and R. Lawson). I thank J. Condit (Ohio State University Museum of Zoology) for access to specimens; the Ohio State University F. T. Stone Laboratory for logistical support; D. Schluter for the cubic spline program; the McTavish family for their hospitality; R. Howard for advice; and G. Arnqvist, R. Kiltie, B. King, S. Scheiner, D. Schluter, and an anonymous reviewer for constructive comments on the manuscript.

#### LITERATURE CITED

- Aleksiuk, M. 1977. Sources of mortality in concentrated garter snake populations. *Canadian Field-Naturalist* 91:70-72.
- Andersson, S. 1992. Female preference for long tails

- in lekking Jackson's widowbirds: experimental evidence. *Animal Behavior* 43:379-388.
- Arnold, S. J. 1983. Morphology, performance, and fitness. *American Zoologist* 23:347-361.
- . 1986. Laboratory and field approaches to the study of adaptation. Pp. 157-179 in M. E. Feder and G. V. Lauder, eds. *Predator prey relationships: perspectives and approaches from the study of lower vertebrates*. University of Chicago Press, Chicago.
- . 1988. Quantitative genetics and selection in natural populations: microevolution of vertebral number in the garter snake *Thamnophis sirtalis*. Pp. 619-636 in E. J. Eisen et al., eds. *Proceedings of the Second International Conference on Quantitative Genetics*. Sinauer, Sunderland, Mass.
- Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38:709-719.
- . 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38:720-734.
- Beatson, R. R. 1976. Environmental and genetical correlates of disruptive coloration in the water snake, *Natrix s. sipedon*. *Evolution* 30:241-252.
- Black, J. H. 1983. Northern water snakes eaten by a channel catfish. *Bulletin of the Oklahoma Herpetological Society* 8:63-65.
- Brodie, E. D., III. 1989. Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides*. *Nature* 342:542-543.
- . 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* 46:1284-1298.
- Brown, E. E. 1940. Life history and habits of the northern water snake, *Natrix sipedon sipedon* Linne. Ph.D. dissertation, Cornell University, Ithaca, N.Y.
- Brown, J. F. 1931a. The visual perception of velocity. *Psychologische Forschung* 14:199-232.
- . 1931b. The thresholds for visual movement. *Psychologische Forschung* 14:249-268.
- Camin, J. H., and P. R. Ehrlich. 1958. Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. *Evolution* 12:504-511.
- Camin, J. H., C. Triplehorn, and H. Walter. 1954. Some indications of survival value in the type "A" pattern of the island water snakes in Lake Erie. *Chicago Academy of Sciences, Natural History Miscellanea* 131:1-3.
- Conant, R. 1951. *The reptiles of Ohio*, 2d ed. University of Notre Dame Press, South Bend, Ind.
- Conant, R., and W. Clay. 1937. A new subspecies of watersnake from the islands in Lake Erie. *Occasional Papers of the Museum of Zoology University of Michigan* 346:1-9.
- Ehrlich, P. R., and J. Camin. 1960. Natural selection in Middle Island water snakes (*Natrix sipedon* L.). *Evolution* 14:136.
- Endler, J. A. 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11:319-364.
- . 1984. Progressive background matching in moths, and a quantitative measure of crypsis. *Biological Journal of the Linnean Society* 22:187-231.
- . 1986. *Natural selection in the wild*. Princeton University Press, Princeton, N.J.
- . 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research* 31:587-608.
- Floyd, C. B. 1933. Further notes on Penikese Island terns. *Bird Banding* 4:200-202.
- Ford, E. B. 1975. *Ecological genetics*, 4th ed. Academic Press, N. Y.
- Goldman, P. 1971. Herring gull predation on common water snake in Lake Erie. *Wilson Bulletin* 83:196-197.
- Guthrie, J. E. 1932. Snakes versus birds; birds versus snakes. *Wilson Bulletin* 44:88-113.
- Hedrick, P. M., M. Ginevan, and E. Ewing. 1976. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics* 7:1-32.
- Hoffman, R. D., and R. D. Curnow. 1979. Mercury in herons, egrets, and their foods. *Journal of Wildlife Management* 43:85-93.
- Jackson, J. F., W. Ingram, and H. W. Campbell. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. *American Naturalist* 110:1029-1053.
- Jayne, B. C., and A. F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204-1229.
- Kiltie, R. A. 1992. Tests of hypotheses on predation as a factor maintaining polymorphic melanism in coastal-plain fox squirrels (*Sciurus niger* L.). *Biological Journal of the Linnean Society* 45:17-37.
- Kiltie, R. A., and A. F. Laine. 1992. Visual textures, machine vision, and animal camouflage. *Trends in Ecology and Evolution* 7:163-166.
- King, R. B. 1986. Population ecology of the Lake Erie water snake, *Nerodia sipedon insularum*. *Copeia* 1986:757-772.
- . 1987. Color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum*. *Evolution* 41:241-255.
- . 1992. Morph and age specific crypsis in Lake Erie water snakes. *Evolutionary Ecology* 6:115-124.
- . 1993. Color pattern variation in Lake Erie water snakes: inheritance. *Canadian Journal of Zoology* 71:1985-1990.
- King, R. B., and B. King. 1991. Sexual differences in color and color change in woodfrogs. *Canadian Journal of Zoology* 69:1963-1968.
- Kingsolver, J. G., and D. W. Schemske. 1991. Path analysis of selection. *Trends in Ecology and Evolution* 6:276-280.
- Kushlan, J. A. 1978. Feeding ecology of wading birds. Pp. 249-297 in A. Sprunt IV et al., *Wading birds*. National Audubon Society, New York.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210-1226.
- Lynch, C. B. 1992. Clinal variation in cold adaptation in *Mus domesticus*: verification of predictions from laboratory populations. *American Naturalist* 139:1219-1236.
- McGrew, W. C. III. 1963. Channel catfish feeding on diamond-backed water snakes. *Copeia* 1963:178.

- Mitchell-Olds, T., and R. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* 41:1149-1161.
- Norusis, M. J. 1988a. SPSS/PC+ V2.0 Base manual. SPSS, Chicago.
- . 1988b. SPSS/PC+ Advanced statistics V2.0. SPSS, Chicago.
- Pough, F. H. 1976. Multiple cryptic effects of cross-banded and ringed patterns of snakes. *Copeia* 1976: 834-836.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution* 42:849-861.
- Sinervo, B. 1990. The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279-294.
- Stebbins, G. L. 1977. *Processes of Organic Evolution*. Prentice-Hall, Englewood Cliffs, N.J.
- Sweet, S. 1985. Geographic variation, convergent crypsis, and mimicry in gopher snakes (*Pituophis melanoleucus*) and western rattlesnakes (*Crotalus viridis*). *Journal of Herpetology* 19:55-67.
- Wade, M. J., and S. Kalisz. 1990. The causes of natural selection. *Evolution* 44:1947-1955.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159.
- . 1988. Surfaces of selective value revisited. *American Naturalist* 131:115-123.

Corresponding Editor: D. Schluter