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Microevolution in Island Water Snakes

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What processes influence color pattern differences in Lake Erie island and mainland water snakes?

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Evolutionary change can result from a variety of processes, including natural selection, gene flow, random genetic drift, and mutation. The potential importance of these processes became clear with the development of mathematical population genetics beginning in the early 1900s (for a historical account, see Provine 1971). Examples demonstrating the effectiveness of these processes in promoting evolutionary change have since accumulated. However, such examples often emphasize a single process, most frequently natural selection (Endler 1986); only in a few examples of microevolutionary change are the simultaneous effects of multiple processes well understood (e.g., McNeilly 1968, Riechert 1993, Ross and Keller 1995). Mode of inheritance of a trait (number of loci, degree of dominance, and epistatic and pleiotropic effects) and population history (changes in distribution and abundance) can also influence evolutionary change, but again, only in a few examples of microevolutionary change are the effects of mode of inheritance and population history well understood. The Lake Erie water snake *Nerodia sipedon insularum* is an example of such a rare case: Color pattern variation in island populations of this snake provide a classic example of microevolutionary change in which the effects of selection, gene flow, inheritance, and population history are unusually well understood (King 1992, 1993a, 1993b, King and Lawson 1995).

> **Evolutionary outcomes depend not only on those processes that operate within populations (e.g., selection) but also on interactions (via gene flow) among populations**

The water snake, *Nerodia sipedon*, is an aggressive but nonpoisonous colubrid snake that occupies aquatic habitats throughout eastern North America (Conant and Collins 1991). Although an adept swimmer that feeds on fish and amphibians, the water snake spends much of its time in terrestrial retreats or basking on overhanging vegetation or shoreline rocks. Throughout most of its range, the water snake is regularly patterned, with alternating dark dorsal and lateral blotches on a lighter background. However, water snakes found on islands in western Lake Erie (Figure 1) are highly variable in color pattern: They range from regularly patterned individuals that are indistinguishable from mainland snakes to uniformly gray, unbanded individuals (Figure 2).

These variations in color pattern initially created confusion over how to classify island water snakes. Clarity was provided by Conant and Clay (1937, 1963), who described island populations of the Lake Erie water snake, *N. s. insularum*, as being distinct from the northern water snake, *N. s. sipedon*. Conant and Clay (1937) also recognized the presence of intermediate and regularly patterned morphs in island populations as evidence of intergradation between the two subsepecies; thus, they identified gene flow as one of the evolutionary processes influencing color pattern variation in island populations.

Evidence that natural selection influences color pattern in Lake Erie water snakes came from Camin and colleagues (Camin and Ehrlich 1958, Camin et al. 1954, Ehrlich and Camin 1960). Because gray, unbanded snakes blend in with the limestone and dolomite shorelines of the islands (Figure 3), these workers suggested that visual predators, such as gulls, herons, and raptors, were less likely to detect unpatterned snakes, giving them a selective advantage over regularly patterned snakes. Conversely, they suggested, regularly patterned snakes were favored in more heavily vegetated mainland habitats, which lack exposed limestone and dolomite (Figure 3). The observation that, on islands, the frequency of regularly patterned individuals is higher among younger than among older snakes supports the hypothesis that selection favors unbanded snakes in island populations. This re-

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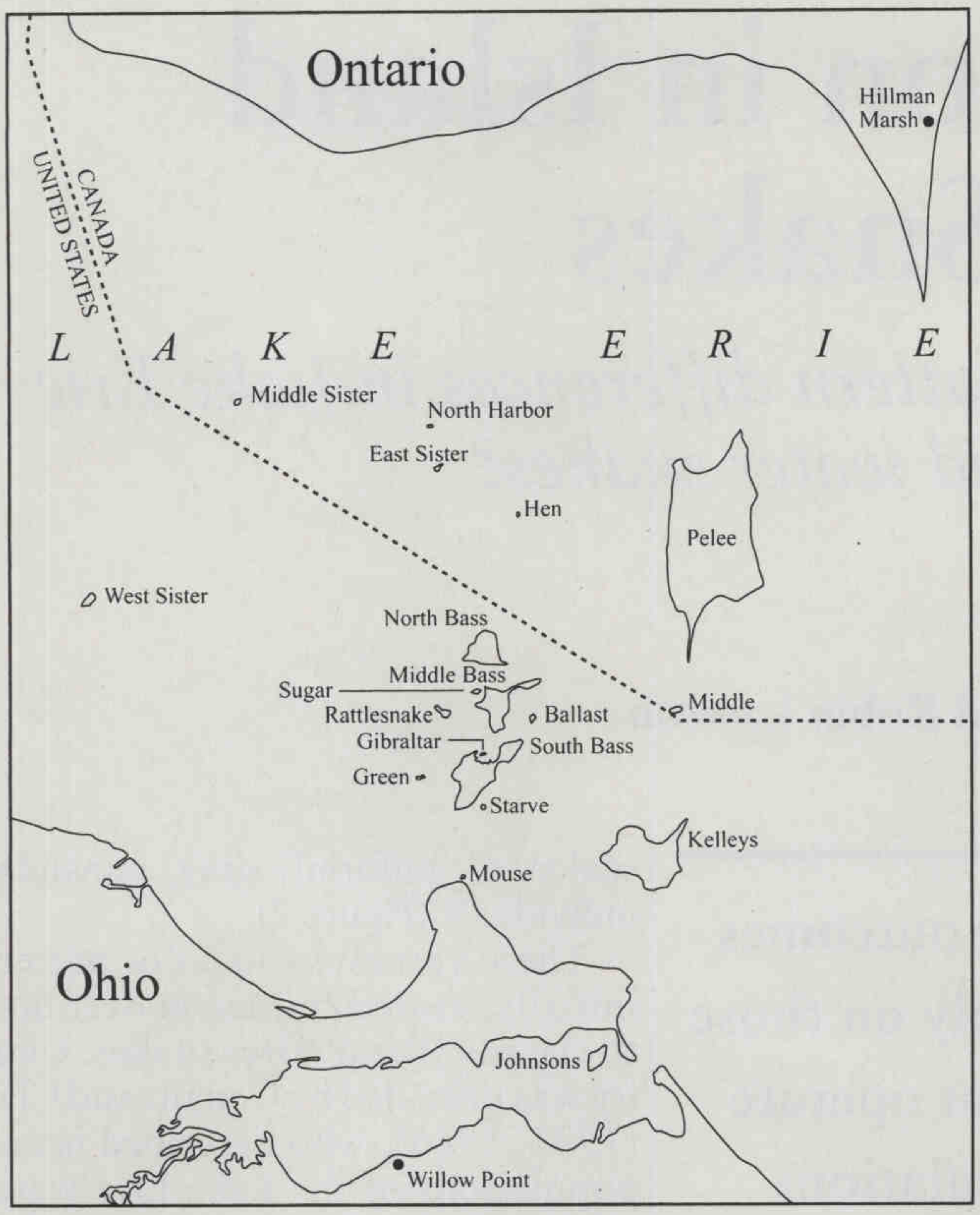

Figure 1. The island region of western Lake Erie. Lake Erie water snakes are known historically from all of the islands shown on the map. Tissue samples used in estimating gene flow came from Hillman Marsh (on the Ontario mainland), Pelee Island, North Bass Island, Middle Bass Island, Rattlesnake Island, Middle Island, and Willow Point (on the Ohio mainland).

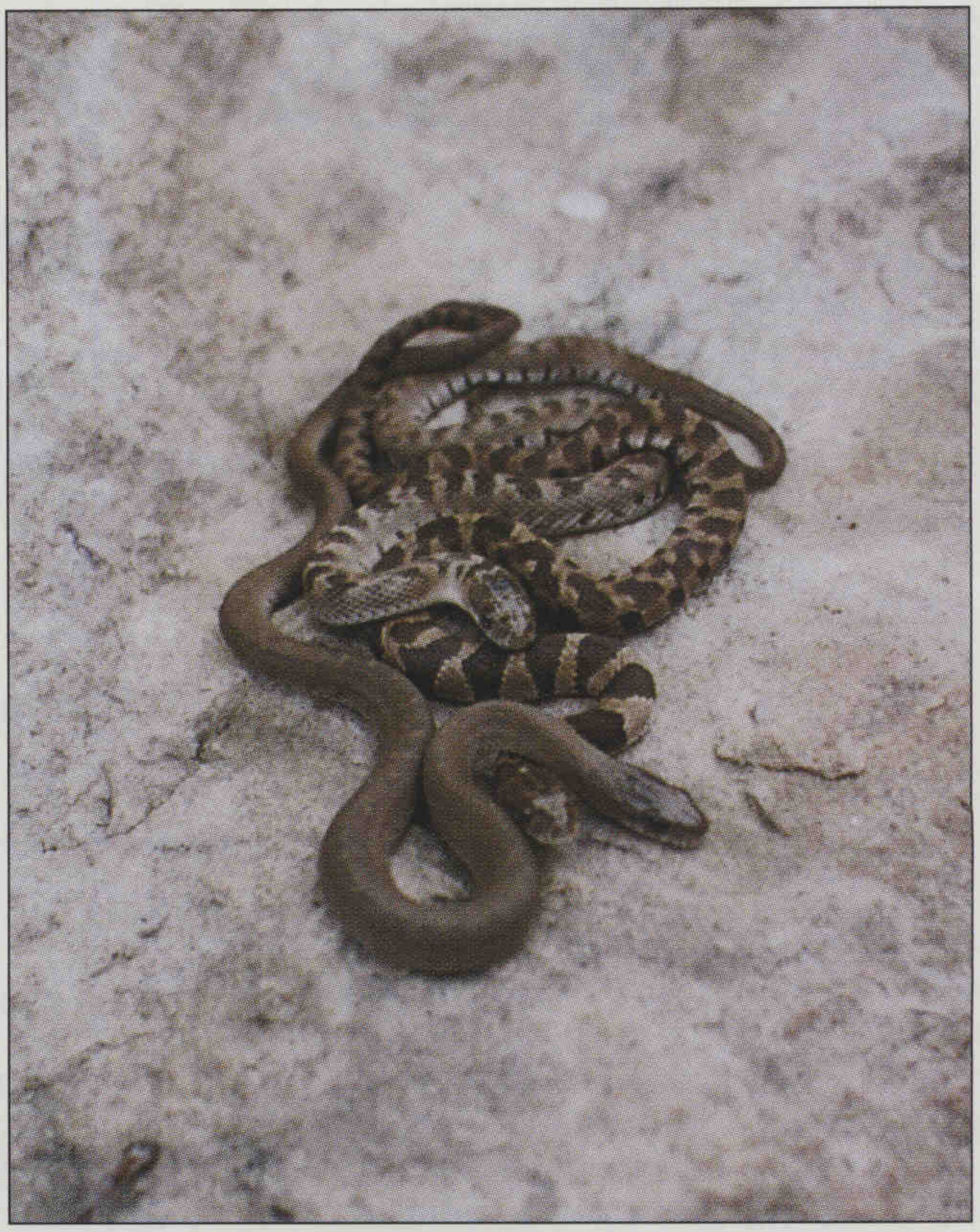

Figure 2. Color pattern variation in Lake Erie water snakes. Regularly patterned snakes (alternating dark dorsal and lateral blotches on a lighter background) are found in both island and mainland populations. Reduced pattern snakes (uniformly gray unbanded morphs and intermediate morphs) are found only in island populations.

sult would be expected if regularly patterned snakes suffered higher mortality (Camin and Ehrlich 1958, Camin et al. 1954, Ehrlich and Camin 1960).

Together, these findings suggest that color pattern variation in island water snake populations results from two processes (Figure 4): natural selection (favoring a reduction in color pattern on islands) and gene flow from mainland populations (allowing regularly patterned snakes to persist on islands). In this article, we provide quantitative estimates of natural selection and gene flow in the Lake Erie water snake and combine these findings with information on inheritance and population history to provide an unusually complete picture of microevolutionary change.

Inheritance

For a trait to evolve, variation in that trait must have a genetic basis. However, establishing a genetic basis is only the starting point for understanding the microevolution of a trait. Evolutionary outcomes are influenced by two additional factors: first, whether variant alleles are additive in their effects on phenotype or display dominance or recessiveness, and second, whether the trait is genetically correlated with other traits through physical linkage or pleiotropy. That is, selection that favors a rare dominant allele will produce more rapid change in allele frequency than selection that favors a rare recessive allele, and selection acting on one trait can result in evolutionary changes in genetically correlated traits, even if those traits do not affect survival or reproduction.

Inheritance is traditionally studied through controlled breeding experiments. For traits exhibiting a few discrete phenotypic classes that are determined by one or a few loci (e.g., flower color in the peas studied by Mendel), such experiments can reveal dominant/recessive relationships among alleles as well as linkage among loci. For traits showing meristic or continuous phenotypic variation that is determined by many loci (e.g., milk yield in dairy cattle), such experiments can be used to estimate heritability, which is a measure of the amount of phenotypic variation that is attributable to genetic (versus environmental) variation (Becker 1992, Falconer 1989).

In organisms, such as water snakes, for which controlled breeding experiments are difficult, information on inheritance can often be obtained by examining patterns of variation within and among groups of relatives. If most of the variation in a trait is genetic, then relatives should resemble one another closely, and heritability should be close to one (a heritability of one means that 100% of the variation has a genetic basis). By contrast, if most of the variation in a trait is environmental, relatives should be no more similar to one another than to nonrelatives, and heritability should be close to zero. This quantitative genetic approach is used routinely by evolutionary biologists, and estimates of heritability are accumulating for a wide variety of traits and organisms.

Quantitative genetic analysis of color pattern variation in the Lake Erie water snake has focused on four components of color pattern: number of dorsal blotches, number of lateral blotches, height of lateral blotches (in scale rows), and extent of the underside of the snake that is pigmented (King 1993a). These components exhibit a broad range of variation, change little ontogenetically, and differ little between males and females. We examined these components and their variation in females and their offspring. Gravid females were collected from island study sites and maintained in captivity until parturition (water snakes, like all other North American natricine snakes, are live bearing), at which time mothers and offspring were scored for color pattern (King 1993a). Heritability estimates of individal components ranged from 0.34 to 0.79, indicating that there is significant genetic variation in color pattern on which evolutionary processes could act. Heritable variation in color pattern components is present in northern water snakes, *N. s. sipedon,* as well (Beatson 1976).

We also found that the different components of color pattern are positively genetically correlated (genetic correlations between pairs of components range from 0.40 to 0.82). This finding indicates that processes resulting in changes in one color pattern component should produce correlated changes in other components (e.g., natural selection for a reduction in number of dorsal blotches should produce a reduction in number of lateral blotches).

If heritability and genetic correlation estimates are to be used to model evolutionary change, then these parameters must remain relatively constant across multiple generations. Such constancy is more likely if traits are determined by many loci, each with a small effect, than if they are determined by one or a few loci, each with a large effect. In the latter case, changes in allele frequency at these loci from one generation to the next will result in changes in heritability and genetic correlation.

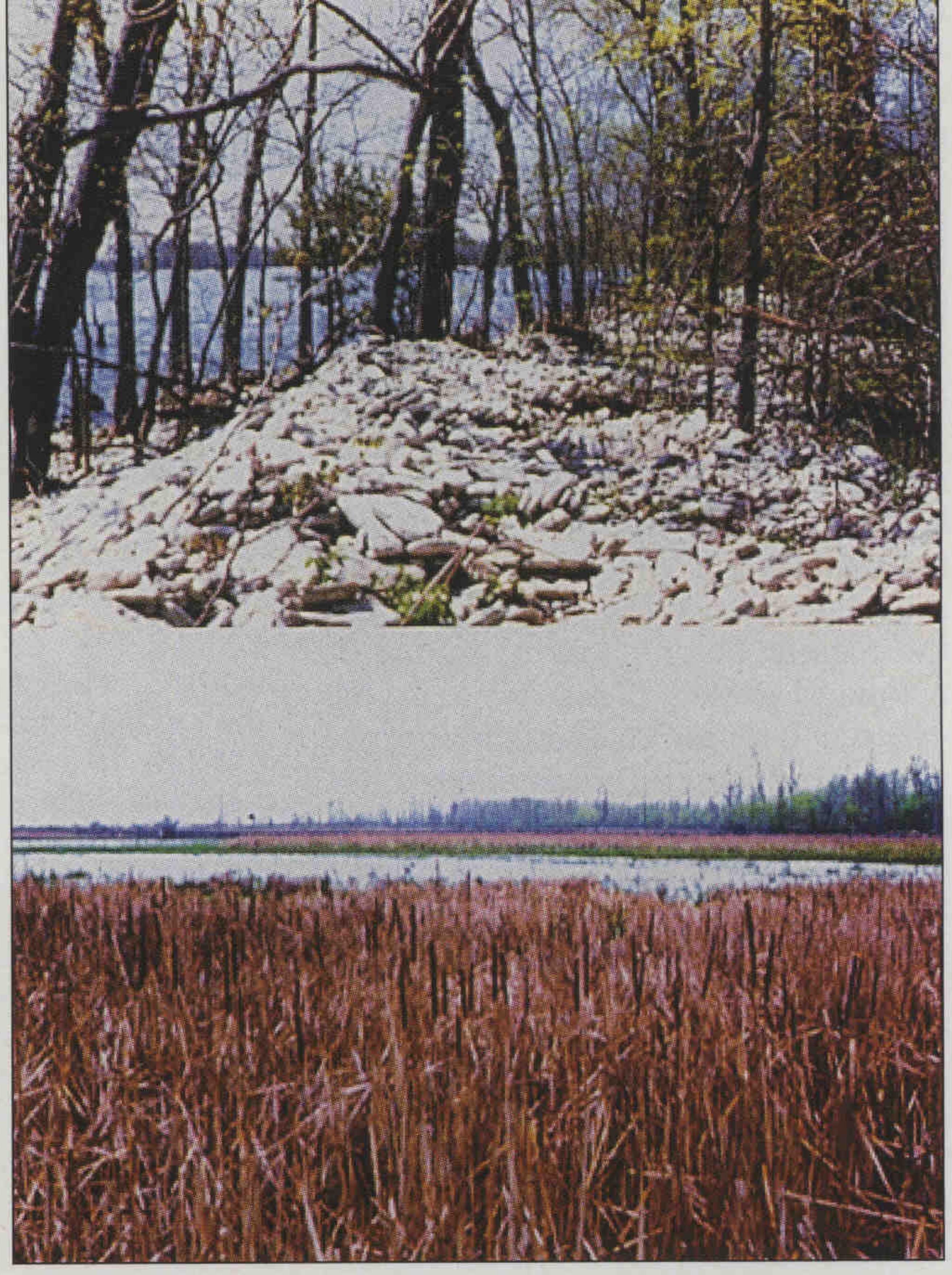

Figure 3. Lake Erie island (top) and mainland (bottom) habitats of water snakes. Uniformly gray unbanded morphs are apparently more cryptic against island backgrounds, whereas regularly patterned morphs are more cryptic against mainland backgrounds.

Two lines of evidence suggest that color pattern in Lake Erie water snakes is influenced by a major locus. First, there is a correlation between within-family means and variances: Families with relatively few dorsal and lateral blotches have high variances, whereas families with many dorsal and lateral blotches have low variances (King 1993a). This result is consistent with one locus having a strong influence on color

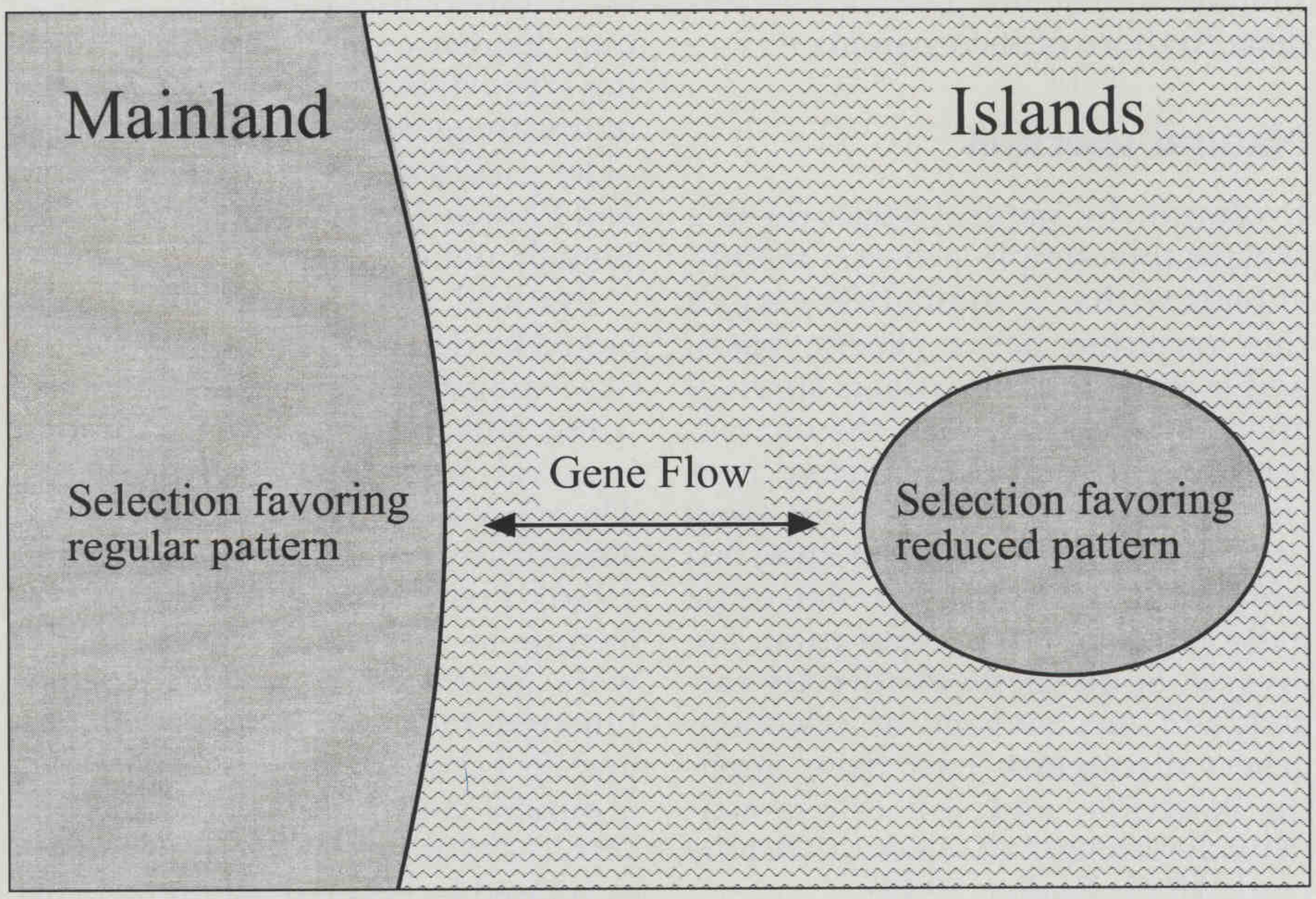

Figure 4. Effects of natural selection and gene flow in Lake Erie water snake populations. Although selection on islands favors snakes with reduced color pattern, gene flow from nearby mainland populations results in the persistence of regularly patterned snakes.

pattern because if one major locus is involved, variation should be greater in families consisting of mixtures of genotypes at this locus than in families consisting mostly of a single genotype at this locus. By contrast, if color pattern were influenced by many minor loci, families should show similar amounts of variation in color pattern.

The second line of evidence comes from the progeny of laboratory crosses between a regularly patterned mainland male and two reduced-pattern island females; these progeny all had the regular color patterns typical of mainland snakes (King 1993a). One way that a major locus might produce these results is if a dominant allele were to result in a regular (mainland-like) pattern, and a recessive allele in a reduced pattern. Families in which most members possess the dominant allele would then have high means and low variances, whereas families in which some members possess this allele and others do not would have lower means and higher variances. Moreover, if the male used in laboratory crosses was homozygous for the dominant allele, then his offspring should all be regularly patterned, regardless of the mother's genotype—exactly the results we obtained. By contrast, if color pattern were controlled by many loci, then offspring should exhibit color patterns intermediate to those of their parents.

Natural selection

Evolution by natural selection is a remarkably simple process: if individuals within a population vary, if this variation has a genetic basis, and if this variation affects survival and reproduction, then the characteristics of that population may change in a predictable way from generation to generation. Despite this simplicity, methods for detecting natural selection in operation are diverse. Some methods identify targets and mechanisms of selection, others distinguish past from ongoing selection, and still others estimate the strength of selection (Brodie et al. 1995, Endler 1986).

One line of evidence that natural selection influences color pattern in Lake Erie water snakes is that differences in color pattern are associated with differences in habitat. Snakes with reduced patterns predominate along the exposed rocky shorelines of the islands, whereas regularly patterned snakes predominate in heavily vegetated mainland marshes (Figure 3). This association between color pattern and habitat suggests both a target (color pattern) and a mechanism (differential predation) of selection. Evidence that selection is ongoing is provided by the comparisons of morph frequency between younger and older snakes described earlier (Camin and Ehrlich 1958, Camin et al. 1954, Ehrlich and Camin 1960).

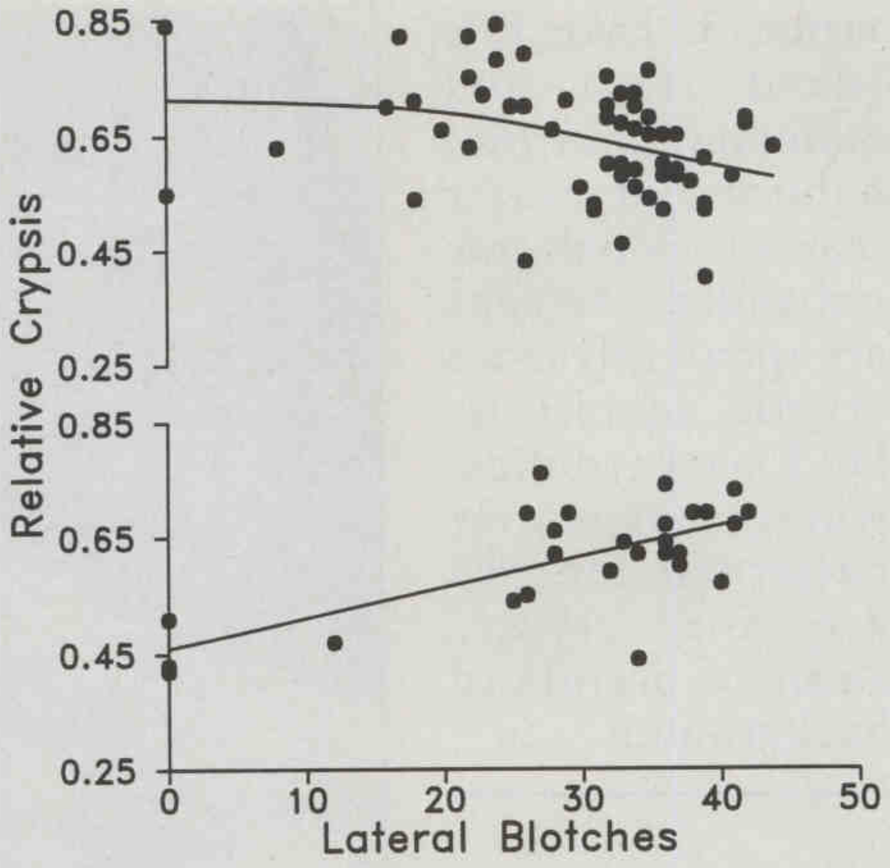

Figure 5. Performance functions relating crypsis and number of lateral blotches in neonates (top) and adult snakes (bottom). Each point represents an individual snake; lines represent the results of nonparametric regression (Schluter 1988). Among neonates, crypsis decreases as the number of lateral blotches increases; however, among adults, crypsis increases as the number of lateral blotches increases.

Natural selection can also be detected by determining how variation in a trait influences performance and using this information to predict survival and reproduction rates. These predictions can then be tested empirically (Arnold 1983, Endler 1986). Predictions about natural selection in Lake Erie water snakes were generated from performance functions relating relative crypsis (the match between snakes and backgrounds) and color pattern (King 1992, 1993b). Relative crypsis was estimated by comparing the size distributions of patches making up snake color patterns with the island background (limestone and dolomite) color pattern. As expected, relative crypsis decreased with increasing color pattern score (e.g., number of lateral blotches) among younger snakes (Figure 5). By contrast, relative crypsis increased with increasing color pattern score among older snakes (Figure 5)—a surprising result given the suggestion by Camin and colleagues (Camin and Ehrlich 1958, Camin et al. 1954, Ehrlich and Camin 1960) that unbanded snakes of all ages were more cryptic. Thus, the direction of natural selection on islands is predicted to differ between younger and older snakes, favoring a reduced color pattern among younger snakes and a regular (mainlandlike) color pattern among older snakes. A similar analysis showed that natural selection is predicted to favor a regular color pattern on the mainland, regardless of age (King 1992).

To test these predictions, we marked and released 317 newborn water snakes from our inheritance study and recaptured 54 of the survivors the following spring and summer (King 1987, 1993b). Such longitudinal data, which provide information on pre- and postselection color pattern frequencies for a single cohort, are valuable because they can be used to directly estimate the strength of natural selection. Longitudinal data on additional cohorts were obtained by taking advantage of the fact that newborns and juveniles fall into discrete body size categories. Thus, newborns sampled in one year and juveniles sampled in the following year represent a single cohort from which pre- and postselection color pattern distributions can be estimated. Four such data sets were collected, numbering from 27 to 68 individuals each (King 1993b).

To test for selection among older snakes, pre- and postselection color pattern frequencies were estimated by simultaneously sampling several cohorts of different ages. Such cross-sectional data can also be used to estimate the strength of selection, assuming that trait frequencies are unaffected by processes other than natural selection (Arnold and Wade 1984). Five cross-sectional data sets were used to test for selection on snakes of different ages, with sample sizes ranging from 16 to 67 juveniles, 24 to 66 subadults, and 73 to 113 adults (King 1993b).

Tests for natural selection center on a simple question: Do trait distributions differ in mean or variance before and after an episode of selection? We found significant color pattern differences between pre- and postselection samples in the mass release experiment and between neonates and juveniles (multivariate analysis of variance, $P = 0.033$ and $P = 0.001$, respectively): Snakes in postselection samples had fewer dorsal and lateral blotches than snakes in preselection samples. Differences between juveniles and subadults and between subadults and adults were not significant ($P = 0.052$ and $P = 0.071$, respectively; King 1993b).

Quantitative information on the form (e.g., directional or stabilizing) and strength of natural selection is provided by selection gradients (Lande and Arnold 1983). These gradients are obtained by using multiple regression to assess the independent effects of each of several traits (in this case, the four color pattern components) on fitness (e.g., whether a snake survived to be recaptured in the mass release experiment). As Table 1 indicates, when we analyzed snake color pattern in this way, we detected the presence of directional selection favoring a decrease in the number of dorsal and lateral blotches among younger snakes (King 1993b). In the mass release experiment, directional selection was sufficient to produce a decrease of approximately 0.3 standard deviation units (i.e., approximately 1.5 blotches) in the number of dorsal and lateral blotches per generation. By contrast, selection gradients among older snakes were close to zero.

The form and strength of natural selection can also be characterized in a graphical way, that is, by plotting fitness functions, which illustrate the relationship between the value of a trait and a measure of fitness (Schluter 1988). In the case of the Lake Erie water snakes, fitness functions corroborate results based on selection gradients: Among neonate and juvenile snakes, fitness functions decrease with increasing numbers of dorsal and lateral blotches; among older snakes, fitness functions show no consistent form for any color pattern component (Figure 6; King 1993b).

Table 1. Directional selection gradients for color pattern components in four age classes of Lake Erie water snakes. Gradients for neonates come from a single data set; those for older age classes represent means of four to five data sets. Data are from King (1993b).

	Color pattern component			
Age class	Number of dorsal blotches	Number of lateral blotches	Height of lateral blotches	Extent of ventral pigmentation
Neonates	−0.30	−0.27	0.01	0.16
Neonate to juvenile snakes	−0.04	−0.12	0.03	0.08
Juvenile to subadult snakes	0.04	−0.06	−0.01	0.02
Subadult to adult snakes	−0.02	0.00	0.01	0.02

Evidence that a major locus determines snake color pattern (see "Inheritance") suggests one final way to characterize selection in Lake Erie water snakes: using data from the mass release experiment to compare the relative survival rate of regularly patterned snakes with that of reduced-pattern snakes. Snakes with regular color patterns had a survival rate just 78%–90% that of snakes with reduced color patterns, giving a selection coefficient, s, of 0.10–0.22 (King and Lawson 1995).

Our conclusion from these analyses is that natural selection favors less patterned water snakes in island populations and that younger snakes are most subject to selection. Among younger snakes, the observed direction of selection corresponds with predictions based on the similarity between snakes and backgrounds, further suggesting that differential predation by visual predators is the mechanism of selection. However, among older snakes, observation (i.e., an absence of selection) does not agree with prediction (i.e., selection for an increase in patterning), most likely because older snakes outgrow their predators. Although birds are sometimes important predators on snakes (Brodie 1993, Jayne and Bennett 1990, Mushinsky and Miller 1993), even large birds, such as gulls, herons, and raptors, would likely find it difficult to subdue an adult water snake (female water snakes frequently exceed 1 m in length and 400 g in mass).

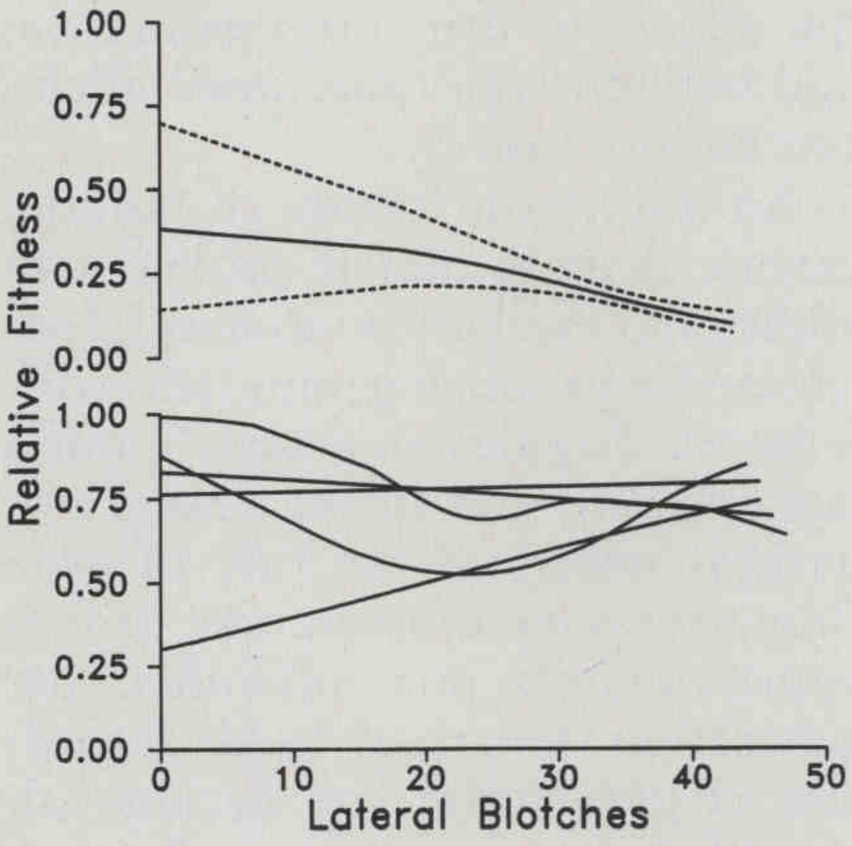

Figure 6. Fitness functions relating survival and number of lateral blotches in neonates (top) and in subadult and adult snakes (bottom). For neonates, dashed lines represent ±1 SE. For subadult and adult snakes, each line represents a different data set. Among neonates, fitness decreases as the number of lateral blotches increases, but among older snakes, no clear relationship between fitness and color pattern is evident.

Gene flow

Gene flow refers to the translocation of alleles from one population to another. In vertebrates, gene flow is accomplished as individuals move from the area of their birth to another area in which they subsequently reproduce. (Gene flow is often referred to loosely as migration, but the latter term has other meanings as well.) The net effect of gene flow is homogenization: In the absence of other processes (e.g., natural selection), gene flow maintains genetic similarity among populations.

Conversely, if gene flow is rare or lacking, then populations may become genetically distinct simply as a result of isolation. This process, which is referred to as random genetic drift, arises because of chance changes in allele frequency from one generation to the next. Random genetic drift is especially evident in small populations, those in which effective population size numbers just tens or a few hundreds of individuals. (Effective population size refers to population size adjusted for age structure, sex ratio, variation in reproductive output, and temporal fluctuations; effective population size is often much smaller than census population size.) Much as a coin tossed only a few times is unlikely to come up heads and tails exactly equally, alleles drawn at random from a gene pool are unlikely to occur at identical frequencies among parents and progeny. But genetic drift differs from coin tossing in that the effects of drift are cumulative, and with enough time, some alleles can be lost entirely.

An important feature of random genetic drift is that it provides an additional mechanism to natural selection for producing population differences. Population genetic models demonstrate that in the absence of natural selection, the rate of gene flow necessary to overcome drift is approximately one individual per generation (this result holds regardless of population size because although drift is greater in small populations, so is the impact of a single immigrant; Slatkin 1987). However, when selection and gene flow occur simultaneously, outcomes are more complex. Selection can prevent population differentiation even when gene flow is rare or produce population differentiation even when gene flow is common. Whether populations become differentiated depends on the strength and direction of selection within populations and on the rate of gene flow among populations. Thus, a clear understanding of the importance of natural selection in population differentiation (e.g., between island and mainland water snake populations) requires information on gene flow.

Rates of gene flow can be estimated directly, by evaluating movement patterns of individual organisms, or indirectly, by assessing the genetic consequences of gene flow (Slatkin 1987). Both of these approaches have strengths and weaknesses, but in organisms for which it is difficult to monitor movement patterns, indirect estimates of gene flow are especially valuable. Indirect methods typically use information on the distribution of genetic markers within and among populations to estimate rates of gene flow. So long as these markers are neutral (i.e., unaffected by natural selection), then differences in their frequencies among populations should be due solely to random genetic drift. Little differentiation suggests that gene flow is common, whereas extensive differentiation suggests that gene flow is rare.

The relationship between population differentiation and gene flow is

$$F_{st} = 1/(1 + 4Nm)$$

where population differentiation is characterized by the fixation index, F_{st}, and gene flow is characterized by Nm, the number of migrants per generation (i.e., the product of effective population size N and rate of gene flow m; Wright 1943, 1969). F_{st} can be obtained from the frequency of neutral markers using the relationship

$$F_{st} = 1 - H_s/H_t$$

where H_s is the frequency of heterozygotes expected within subpopulations if there were no gene flow, and H_t is the frequency of heterozygotes expected in the total population if there were no population subdivision. When gene flow among subpopulations is rare, H_s is small relative to H_t, and F_{st} is large.

Estimates of Nm are sufficient to determine whether random genetic drift alone could produce observed differences between populations. Provided that Nm is less than one individual per generation, drift can be a potent cause of population differentiation (Slatkin 1987). However, to determine whether gene flow is sufficient to balance selection, estimates of m—independent of N—are needed. Such estimates of m are possible for Lake Erie water snakes by using independent estimates of adult population size (King 1986).

For estimating gene flow, any of a variety of genetic markers could be used, but many estimates are based on allozymes detected by gel electrophoresis. Allozymes are variant forms of specific proteins that differ in amino acid sequence as a result of differences in DNA sequence; they are useful in estimating gene flow because many allozymic variants appear to be selectively neutral and it is easy to score the genotypes of large numbers of individuals. To estimate gene flow among water snake populations, we collected blood and muscle samples (nondestructively) at five island and two mainland sites (Figure 1). Sample sizes ranged from 25 to 110 individuals per site. We scored individual genotypes for seven polymorphic proteins, each represented by two or three alleles. Two lines of evidence suggest that these proteins are selectively neutral: genotypic frequencies within populations did not deviate significantly from Hardy-Weinberg expectations ($P > 0.05$), and estimates of F_{st} were similar for all seven proteins (if a protein was under selection, then its F_{st} would differ markedly from that of other neutral markers; Slatkin 1987). Estimates of Nm varied from 2.4 to 53.1 individuals per generation between pairs of sites (King and Lawson 1995); Nm decreased as the distance between two sites increased (King and Lawson 1995), as expected with populations that are isolated by distance (Slatkin 1993).

To estimate the rate of gene flow (m) from Nm, we treated the islands as a unit and calculated mean Nm between the Ohio mainland and the islands (3.6 individuals per generation) and between the Ontario mainland and the islands (9.2 individuals per generation). We then added these values to obtain an overall estimate of Nm between the mainland and the islands of 12.8 individuals per generation. Treating islands as a unit is justified because rates of gene flow among islands are high (6.9–53.1 individuals per generation), and as a result, genes translocated from the mainland to one island will end up on other islands as well.

Using a recent estimate of adult island water snake population size (N = 1262), m was calculated to be 0.01 (King and Lawson 1995). However, because water snake populations have decreased during this century (King 1986), we may have underestimated historical values of N and, consequently, overestimated m. To estimate m prior to recent population declines, we multiplied the total length of shoreline on all islands by the mean number of adult water snakes per km of shoreline at sites at which snake density remains high. These calculations yielded an estimate for N of 16,016 adult snakes and an estimate for m of 0.0008.

Thus, our analysis of allozyme variation indicates that at each generation, 0.08%–1% of the island water snake population is replaced by mainland individuals.

Synthesis

Do inheritance, selection, gene flow, and population history adequately explain color pattern differences between island and mainland water snake populations? To answer this question, we used a simple island–continent model, in which islands were treated as a single genetic unit, to simulate color pattern evolution in island populations (King and Lawson 1995). Different forms of this model were used to examine two alternative modes of color pattern inheritance: Mendelian inheritance, in which a reduced color pattern is recessive to a regular color pattern (see "Inheritance"), and quantitative inheritance, in which the color pattern components represent four genetically correlated heritable traits. Estimates of the strength of selection and rate of gene flow came from the analyses described in the previous sections.

The geological history of the Lake Erie region indicates that island and mainland water snake populations were separated by rising water levels approximately 4000 years ago (Calkin and Feenstra 1985). This time period translates into approximately 1000 water snake generations and provides a time frame both for the evolution of island–mainland color pattern differences and for our simulations.

With Mendelian inheritance, if the frequency of the reduced pattern allele on the islands in any generation is q, then the change in allelic frequency from one generation to the next, Δq, is given by the following equation (Hartl and Clark 1989, p. 310):

$$\Delta q = \left[\frac{q - hq^2}{1 - hq^2} - q\right] - mq$$

where h (a measure of the strength of selection) = 1 – (1/[1 – s]); s is the selection coefficient, and m is the rate of gene flow. When the previously calculated values for s (0.1–0.22) and m (0.0008–0.01) are used, we found that after 1000 generations, the frequency of the reduced pattern allele should exceed 50% (our lowest estimate of the frequency of the reduced pattern allele on any island). However, this was true only when we used an initial frequency for the reduced pattern allele of 0.5% or greater. This initial allele frequency is greater than that expected from mutation alone, suggesting that some other evolutionary process (e.g., random genetic drift, inbreeding, or founder events) may have been necessary to "kick start" the process of island–mainland differentiation. One possibility is that island formation resulted both in a habitat change that favored reduction in color pattern and in a population subdivision that was necessary for the initial increase in the frequency of the reduced-pattern allele. This combination of random genetic drift followed by directional selection is much like the process envisioned by Wright (1931, 1988) in his shifting balance theory of evolution.

With quantitative inheritance, the change in a suite of character values from one generation to the next is

$$\Delta \mathbf{z} = \mathbf{G}[\boldsymbol{\beta}(1 - m) - \mathbf{d}m]$$

where $\Delta \mathbf{z}$ is a vector of change in trait means; $\mathbf{G}$ is the genetic variance–covariance matrix, which describes heritabilities and genetic correlations among a suite of characters; $\boldsymbol{\beta}$ is a vector of standardized selection gradients; m is the rate of gene flow; and $\mathbf{d}$ is a vector of trait differences between island and mainland populations. Using $\mathbf{G}$ from the analysis of inheritance, $\boldsymbol{\beta}$ from the mass release experiment, and m = 0.01–0.0008, we found that after 1000 generations the mean number of dorsal and lateral blotches was expected to be lower in island than in mainland water snake populations.

Although the direction of this expected difference was consistent with observed differences between the island and mainland populations, its magnitude was much greater than observed differences. One reason for this inconsistency may be that in our simulation, genetic variances and covariances, selection gradients, and gene flow remained constant through time. This may not be true in nature. For example, if a major locus influences color pattern, and if the frequency of the reduced pattern allele was initially low at this locus, then heritability of color pattern (and, consequently, the rate of color pattern evolution) would have been lower immediately following isolation of island populations than at present. Alternatively, the effects of selection on color pattern may be more complex than the directional selection gradients described here suggest. For example, in some garter snakes, color pattern and escape behavior are genetically correlated, and the direction of selection on color pattern depends on the type of escape behavior an animal uses (Brodie 1992).

Our simulations demonstrate that the differences in color pattern observed between island and mainland water snake populations could have arisen as a result of observed patterns of selection and gene flow. However, these simulations also suggest that our understanding of the processes influencing color pattern differences in Lake Erie island and mainland water snake populations is incomplete. For differentiation to occur under the Mendelian inheritance model, some other process (e.g., drift) is required for the frequency of the favored allele to increase sufficiently for selection to be effective. Under the quantitative genetic model, expected differentiation between island and mainland populations far exceeds that observed. Clearly, additional information (e.g., on mode of inheritance, on the temporal constancy of selection, and on gene flow) would aid in refining these models.

The example of color pattern evolution in Lake Erie water snakes is unusual in that we have quantitative measures of inheritance, natural selection, gene flow, and population history. Although it is rare to have such complete data on multiple evolutionary processes for a single species, the simultaneous effects of multiple processes probably influence patterns of variation in many organisms. Lake Erie island and mainland garter snake populations are also variable in color pattern, consisting of typical striped morphs and jet-black melanistic morphs. As in Lake Erie water snakes, gene flow is common among garter snake populations; however, despite high rates of gene flow, frequencies of striped and melanistic garter snakes differ between populations, suggesting that selection favors differenct morphs in different habitats (Lawson and King 1996).

Opposing effects of natural selection and gene flow are also evident in desert spiders and perennial grasses. Natural selection favors different behavioral genotypes in spiders and different metal-tolerance alleles in grasses in adjacent habitats, but in both cases gene flow between habitats prevents fixation of alleles favored in one habitat or the other (McNeilly 1968, Riechert 1993). Similarly, social interactions result in strong directional selection on alleles at the *PGM-3* locus (which encodes phosphoglucomutase) in some fire ant colonies, but again, gene flow, in this case from colonies of a different social form, prevents fixation of the favored allele (Ross and Keller 1995).

These examples demonstrate that evolutionary outcomes depend not only on those processes that operate within populations (e.g., selection) but also on interactions (via gene flow) among populations. Thus, factors affecting rates of gene flow are likely to produce evolutionary change even when within-population processes remain constant. These examples also illustrate that the combined effects of selection and gene flow are not restricted to organisms found on islands like those in western Lake Erie but may be important in any organism whose distribution spans a range of habitat types. As human activities produce changes in habitat characteristics and distribution (e.g., by fragmenting formerly continuous habitats), changes in selection regimes and rates of gene flow may produce microevolutionary changes in other organisms that mirror those seen in island water snakes.

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