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Population Genetics of the Slider Turtle

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Abstract

Genetic data necessary for defining population structure in *T. scripta* were collected through starch gel electrophoresis, which permits visualization of Mendelian inherited gene products (proteins) found in various body tissues. The available genetic data are summarized, and documentation is given that populations are not genetically homogeneous temporally, spatially, or among demographic subgroups. The slider turtle appears to be one of the most genetically variable vertebrates. Possible explanations are given for the existence of both spatial genetic differentiation and high dispersal rates among populations of *T. scripta*. Dispersal, stochastic events, and natural selection interact to produce a series of populations that are in a state of dynamic disequilibrium and are dramatically affected by environmental conditions such as droughts. The suggestion is made that the observed genetic disequilibrium may occur generally in vertebrates, especially those with short life cycles, resulting in more opportunities for rapid genetic changes to local environmental differences. The influence of genetics, environmental factors, and their interactions on population dynamics needs to be evaluated within a regional context to obtain a better understanding of the genetically dynamic nature of this species.

Introduction

The slider turtle (*Trachemys scripta*) is a long-lived species that has been extensively studied on the Savannah River Plant (SRP) for the last 20 years. Many aspects of its population biology are associated with its longevity, long generation time, and overlapping generations (Gibbons and Semlitsch, 1982; Gibbons, 1987). These characteristics make populations relatively slow to respond to environmental pressures for evolutionary change, because they increase the length of time needed for the population to turn over. These demographic parameters are well documented for a number of populations on the SRP. Popula-

tions occur in a variety of natural and disturbed habitats and vary in their age structures, reproductive characteristics, and growth patterns (Gibbons et al., 1981; Gibbons and Semlitsch, 1982). The genetic characteristics of populations on the SRP are less well known (Scribner et al., 1986), but the pattern for both the genetic and the demographic characteristics is one of strong interpopulational differentiation over the SRP (Gibbons et al., 1981; Congdon and Gibbons, 1983; Congdon et al., 1986; Scribner et al., 1986). Significant differences are observed even though the distances between suitable habitats are often relatively small and turtles frequently disperse between them (Gibbons, 1970d; Morreale et al., 1984). Further quantification of the intra- and interpopulation genetic variation is a logical extension of previous work and is needed to understand the microgeographical differentiation of this species within its patchy environment (Levins, 1968).

Genetic differentiation can also be found among various subgroups within a population (e.g., males and females, or young and old), which are often assumed to be genetically equivalent. In other words, the populations are frequently assumed to be panmictic, with the subgroups having the same allelic and genotypic frequencies. For a number of vertebrates this is clearly not the case. Allele frequencies and/or heterozygosities vary according to age (Tinkle and Selander, 1973; Chesser et al., 1982; Scribner et al., 1985; Al-Hassan et al., 1987), sex (Manlove et al., 1975), sex ratios (Simanek, 1978), or body size (Avise and Smith, 1974; Smith and Chesser, 1981; Feder et al., 1984). Such genetic heterogeneity within populations is not normally expected for long-lived vertebrate species exhibiting high vagility and where extensive interbreeding is expected to occur within the population. In addition to the intrapopulational breeding structure, populations interact with others in adjacent areas through dispersal and gene flow. This exchange not only adds or subtracts numbers from the population through immigration and emigration (Lidicker, 1975) but also influences the genetic characteristics of the resulting offspring. A species with high dispersal rates should be characterized by genetic homogeneity over space and among the demographic units within populations unless some other factor or factors, such as strong selection or drift, are acting concurrently. Such a high degree of genetic variation within and among populations may be common, and the approach to genetic equilibrium may be slow in a long-lived species such as *T. scripta*. Environmental perturbations, which may promote large-scale dispersal, local selection, or extreme fluctuations in population size, may prevent equilibrium from ever being attained. The first step in understanding such a potentially dynamic system is to document the existing spatial genetic pattern of the populations.

Genetic data necessary for defining population structure in *T. scripta* were collected through starch gel electrophoresis (Scribner et al., 1986). This technique allows for the visualization of Mendelian inherited gene products (proteins) found in various body tissues. Samples such as blood, liver, and muscle were taken from dissected turtles, or blood and tail muscle were obtained from live turtles that were then released. Variation in general proteins and metabolic enzymes was quantified on starch gels using appropriate stains. With this method, a series of bands are produced, which are interpreted using existing literature on biochemical variation and information on protein quaternary structure. Data consist of allelic and genotypic frequencies and heterozygosities for a number of loci. Single-locus heterozygosity (h) is a measure of the proportion of individuals in a sample that received a different allele from each parent. Multilocus heterozygosity (H) is the average of the single-locus heterozygosities. Available demographic data were taken during mark-release studies or from dissected turtles (Scribner et al., 1986).

Our objective is to summarize the available genetic data for *T. scripta* and to document how the genetic characteristics vary among populations at various times and among demographic subgroups within populations. Specifically, we want to illustrate how the genetic characteristics vary (1) over space as a function of geographical distance among collecting sites, (2) over years, or (3) among turtles of differing ages or sexes. Nineteen loci have been studied for variation in 16 populations, and 1 additional locus was analyzed for only 4 populations (Table 6.1). Collecting sites were on or near Aiken, South Carolina, on the SRP (Fig. 6.1). These data for populations within the Lost Lake System (1 = Seepage Basin, 2 = Lost Lake, 3 = Steed Pond, and 4 = Lodge Lake), Par Pond, and Oxbow Lakes have been previously published (Scribner et al., 1984b, 1986). Data from all 19 loci for Cecil's Pond, Pond B, Ellenton Bay, and Steel Creek are reported here for the first time.

Trachemys scripta appears to be genetically more variable than the majority of reptiles and vertebrates in general (Nevo et al., 1984). Genetic variability is often reported as H. Reptiles have an H of .060 ± .053 (SE), and *T. scripta* has an H of .127 ± .045 (Table 6.1). The overall estimate for reptiles contains data for very few turtles: *Sternotherus odoratus*, H = .080–.138 (Seidel et al., 1981); *Caretta caretta*, H = .019–.022; and *Chelonia mydas*, H = .000–.135 (Smith et al., 1977; Bonhomme et al., 1987). Additional multilocus studies in turtles have been conducted using electrophoretic techniques without estimating H (Crenshaw, 1965; Karig and Wilson, 1971; Merkle, 1975; Vogt and McCoy, 1980; Seidel and Lucchino, 1981; Sites et al., 1981; Derr et al., 1987; Seidel and Adkins, 1987). The percent polymorphic loci (P) and alleles per locus (A) also tended to be high in *T. scripta* (Table 6.1). These estimates of genetic variability would be expected to change if additional loci were studied (Gorman and Renzi, 1979). How-

Table 6.1. Measures of the variability for 19 loci in *Trachemys scripta* on or near the Savannah River Plant

Locus (abbreviation)	Allele designations[a]	Number of alleles	Mean single-locus heterozygosity (h)[b]	Number of populations	F_{st}[c]
Creatine kinase (*Ck*)-1	100	1	.000	16	.000
Ck-2	100	1	.000	16	.000
Ck-3	100	1	.000	16	.000
Glucose phosphate isomerase (*Gpi*)-1	100,105,98[d]	3	.489	16	.022
Fumarase (*Fh*)	100	1	.000	16	.000
Isocitrate dehydrogenase (*Icd*)-1	100,104,94	3	.332	16	.057**
Icd-2	100,109,95	3	.273	16	.083**
Lactate dehydrogenase (*Ldh*)-1	100	1	.000	16	.000
Ldh-2	100,88	2	.004	16	.059**
Malate dehydrogenase (*Mdh*)-1	100,92,85,78	4	.648	16	.025
Mdh-2	100,58	2	.014	16	.018
Malic enzyme (*Mod*)-1	100,94	2	.006	16	.074**
Mod-2	100,115	2	.395	16	.026
Mannose-6-phosphate isomerase (*Mpi*)	100,91,110	3	.042	16	.136**
Nucleoside phosphorylase (*Np*)	100,112,89	3	.026	16	.022
Peptidase (*Pep*)-1	100	1	.000	4	.000
Phosphoglucomutase (*Pgm*)-1	100,107,92	3	.105	16	.032*
6-Phosphogluconate dehydrogenase (6-*Pgd*)	100,112,89	3	.535	16	.089**
Protein (general; *Pt*)-2	100,86	2	.089	16	.038*
Mean		2.33 ± 0.23 (A)	.127 ± .045 (H)		.048**

Abbreviations: A, alleles per locus; H, multilocus heterozygosity; h, single-locus heterozygosity.

[a]Alleles are listed from left to right in terms of their frequencies across populations with the common allele as 100.

[b]Percent polymorphic loci (P) at the .01 level of significance = 57.9 and at the .05 level of significance = 47.4.

[c]Measure of divergence at individual loci among populations (Nei, 1978).

[d]Only one turtle was observed with this allele.

*$p \leq .05$ for test of $F_{st} = 0$.

**$p \leq .01$.

ever, the conclusion that *T. scripta* is a highly variable vertebrate is likely to be correct (Nei, 1978). Seidel et al. (1981) have suggested that differences in H among turtle taxa are related to the propensity for both aquatic and terrestrial existence, with habitat generalists having high H. The high variability of this species makes it ideal for population-level studies.

Multilocus heterozygosity showed significant differences among locations with the value for Par Pond 3 (H = .105) being only 55% of that for Oxbow Lake 3 (H = .190), which was the highest value recorded. Large differences in H occurred even over short distances within the continuous aquatic habitat of the Par Pond Reservoir (Fig. 6.1). The lowest H within the reservoir was only 67% of the highest value. Such differences are normally seen only over larger geographical distances in vertebrates and imply microgeographical structuring. There was also significant differentiation in allele frequencies among the samples for *Icd*-1, *Icd*-2, *Ldh*-2, *Mod*-1, *Mpi*, 6-*Pgd*, *Pgm*-1, and *Pt*-2, which included all of the highly variable loci ($h > .100$) except *Gpi*-1, *Mdh*-1, and *Mod*-2 (F statistics, Table 6.1). The spatial heterogeneity was also significant when considered across all loci (F_{st} = .048). The observed levels of genetic heterogeneity suggest that the samples are not panmictic but rather represent disjunct breeding groups. The number of populations on the SRP cannot be determined from these data but is probably quite large. Locations that are close together can have turtles with significantly different genetic characteristics (e.g., 6-*Pgd*, Fig. 6.1). Thus, populations are structured on a microgeographical scale, and the causes and consequences of this structure could be important in influencing the population dynamics of this species.

Dispersal is an important process in determining gene flow among local populations. When gene flow is high and random with respect to the genotypes of the dispersing individuals, the probability of differentiation is low (Crow and Kimura, 1970; Brown, 1985). The amount of movement and presumably gene flow between local populations of *T. scripta* and related species seems quite high (Gibbons, 1970d; MacCulloch and Secoy, 1983b; Morreale et al., 1984; Parker, 1984). One consequence of high amounts of gene flow should be that allele frequencies of adjacent populations are similar and show positive correlation. There is a trend for significant spatial autocorrelation between allele frequencies at interpopulational distances up to 6 km (Fig. 6.2). The influence of gene flow becomes negligible at interlocation distances of 6 to 8 km.

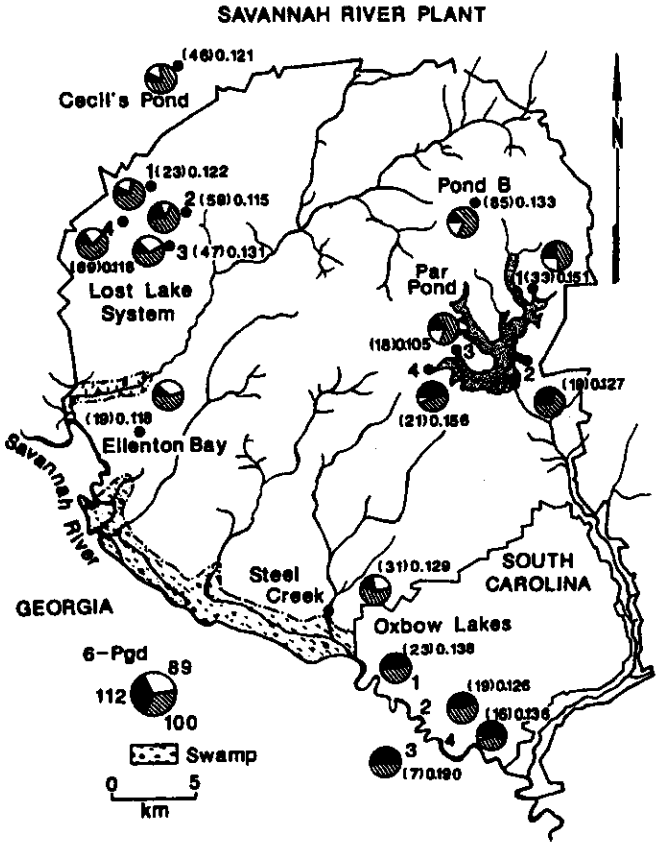

FIGURE 6.1. The locations of 16 sampling sites for *Trachemys scripta* on the Savannah River Plant are given as solid dots. Sample sizes are given in parentheses followed by multilocus heterozygosity (H). The proportions of the circles shaded differentially indicate the frequencies of the three alleles for 6-phosphogluconate dehydrogenase in 1983.

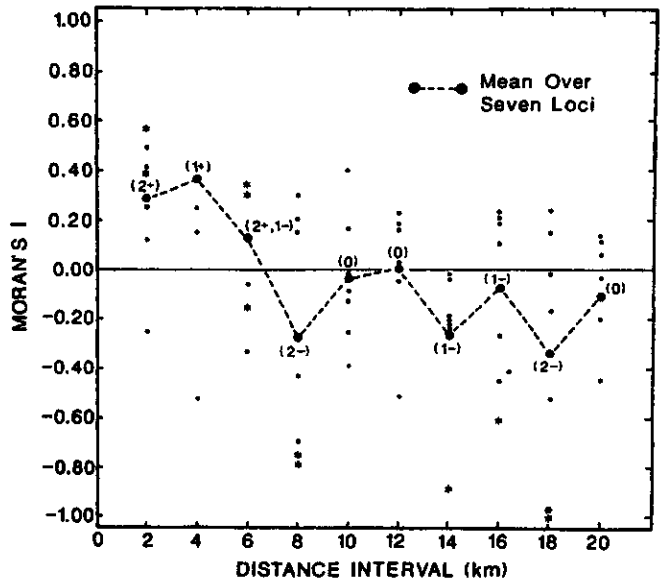

FIGURE 6.2. Results of spatial autocorrelation (Sokal and Oden, 1978) with Moran's I given for various intervals of distance between turtle sampling sites (Fig. 6.1). I is a type of correlation coefficient and varies from -1 to $+1$, with the sign indicating the direction of association. I was calculated from the common allele frequencies for the seven most variable loci listed in Table 6.1. The numbers in parentheses indicate the number and direction of significant associations for particular loci. Significance ($p \leq .05$) for I is indicated by asterisks.

The degree of spatial autocorrelation does not decrease until the interlocation distances exceed 4 to 6 km. Gene flow is of a magnitude such that samples taken within 4 km of each other are genetically homogeneous. Effective gene flow appears to be occurring over greater distances than the observed mean individual dispersal distance among the locations of the Lost Lake System ($\bar{x}$ = 1.84 km; Morreale et al., 1984). The distance of positive association should be strongly influenced by the type of intervening habitat as well as by other factors that influence dispersal of turtles; it represents the cumulative effects of gene flow averaged over many generations and is much greater than the mean dispersal distance observed during any one generation.

Significant spatial autocorrelation and differentiation seem contradictory, and perhaps a conclusion of relatively high gene flow among local populations is erroneous. For example, large amounts of movement between local populations may not result in gene flow, because individuals may not breed in the new populations that they enter. Additional evidence for relatively high gene flow is seen in a high prevalence of occurrence of alleles across all 16 locations (Fig. 6.3). Alleles with only moderate frequencies are found in relatively high proportions of the populations. Only one individual per generation need disperse

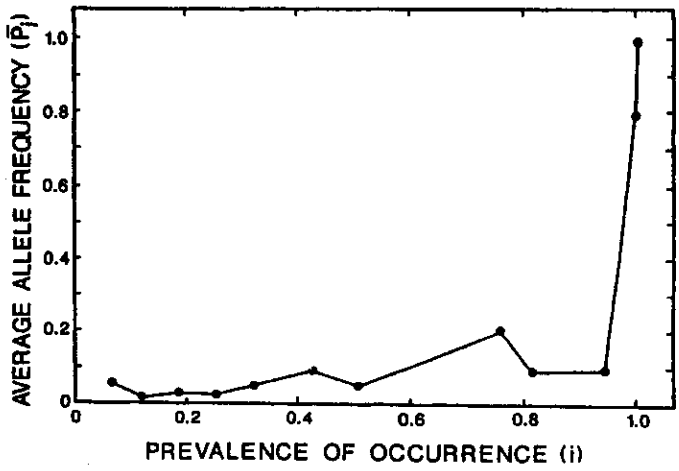

FIGURE 6.3. The unweighted mean frequency of an allele ($\bar{P}_i$) over the 16 samples (Fig. 6.1) as a function of the proportion of the samples in which it occurred (i), as calculated in Slatkin (1981).

Table 6.2. Frequencies of alleles for four variable loci at four locations from which turtles were sampled during 1974 and 1983

		Locations											
		Lost Lake			Steel Creek			Oxbow Lakes			Ellenton Bay		
Locus	Allele	1974	1983		1974	1983		1974	1983		1974	1983	
Gpi	105	.000	.106		.115	.167		.065	.152		.188	.028	
	100	.704	.670	*	.692	.617	NS	.677	.565	NS	.609	.694	*
	98	.296	.223		.192	.217		.258	.283		.203	.278	
Pgm-1	107	.135	.043		.154	.067		.000	.065		.097	.028	
	100	.865	.957	*	.846	.933	NS	.988	.935	*	.903	.972	NS
	92	.000	.000		.000	.000		.032	.000		.000	.000	
Icd-2	109	.000	.053		.000	.050		.000	.023		.000	.139	
	100	1.000	.766	**	1.000	.883	NS	.929	.841	NS	.100	.556	**
	95	.000	.181		.000	.067		.071	.136		.000	.306	
6-*Pgd*	112	.037	.125		.038	.161		.000	.474		.000	.167	
	100	.815	.569	*	.692	.571	NS	.883	.526	**	.438	.536	*
	89	.148	.306		.269	.268		.117	.000		.563	.278	

Note: Significant differences were found in allele frequencies between years in 8 of 16 tests. Abbreviations: Locus abbreviations are given in Table 6.1; NS, $p > .05$.
*$p \leq .05$.
**$p \leq .01$.

between populations to maintain their qualitative equivalence (Wright, 1931), although many more are needed to maintain quantitative equivalence of allele frequencies (Allendorf, 1983). Figure 6.3 presents results similar to those of a simulation model using a migration rate (mN; Slatkin, 1981) of approximately 1.25 to 5 per generation, where N is the number of individuals in the population, and m is the proportion that disperses or migrates. The migration rate can also be calculated from the F_{st} value for each locus or from the overall mean of all loci (.048, Table 6.1); mN is 4.21 per generation, using this method (Wright, 1943). The approximate concordance of these estimates of mN and their large values indicate relatively high gene flow among turtle populations that occur even among discontinuous aquatic habitats. These estimates are averages for the populations, and the rates are probably much higher for some sex-age classes than for others (Morreale et al., 1984; Parker, 1984).

The existence of spatial genetic differentiation among samples, in spite of evidence for high dispersal rates, requires further explanation. Genetic differences could arise by chance in small populations or during severe fluctuations in numbers of effective breeders and then be amplified by drift during subsequent population expansion. These differences, once established in a local population, could require many years of random mating and dispersal to ameliorate, although the local populations could each be in approximate Hardy-Weinberg equilibrium. Populations on the SRP could contain many local subunits that deviate from the mean genetic characteristics of the populations throughout the region, though deviations could continually move toward the average condition by random mating and dispersal within the effective dispersal distance. There is evidence that the genetic characteristics of populations of *T. scripta* are in a state of change on the SRP.

The genetic characteristics of populations on the SRP change over time. Four populations were sampled in 1974 and 1983 for a limited set of loci (Scribner et al., 1984b, 1986). Four of these loci exhibited sufficient variability to warrant testing for significant temporal differences in allele frequencies. Three of the four populations showed significant temporal variations in allele frequency (Table 6.2). Differences are too great for these effects to be interpreted as being caused by chance alone (Sokal and Rohlf, 1969). The genetic characteristics of these populations were temporally transient over this period.

Temporal variation has also been observed for *T. scripta* populations over much shorter intervals. A large number of *T. scripta* were sampled from Pond B during 1983 and 1984 to test for significant temporal shifts in genetic characteristics and changes associated with age for the 19 loci listed in Table 6.1. Younger and older turtles have fewer alleles per locus than those of intermediate ages (A, Table 6.3). The trend for H is different, with the most homozygous turtles being the youngest, whereas the most heterozygous ones are the oldest (2, 3, and 4 years of age, $H = .114$; 4 to 7+ years of age, $H = .144$). The common allele frequencies for the 2 loci chosen to illustrate the maximum differences over age classes were both significantly different, the heterogeneity being due to the differences in the turtles of the 2- and 3-year-old classes. The mean F_{st} associated with age (.050, Table 6.3) is slightly larger than that across the 16 populations (.048, Table 6.1).

Data were also collected from Lost Lake and Steed

Table 6.3. Selected age-specific genetic characteristics for five age classes of *Trachemys scripta*

Age (years)	Number of turtles	Mean multilocus heterozygosity[a]	Mean alleles per locus (A)[b]	Common allele frequency[c]	
				6-*Pgd*	*Mdh*-2
2,3	12	.115	1.67	.364	.800
4	26	.113	1.89	.690	.455
5	19	.133	1.78	.611	.306
6	14	.158	1.83	.500	.500
7,7+	12	.144	1.66	.773	.409

Note: Turtles were collected in Pond B during 1983 and 1984. Loci abbreviations are given in Table 6.1.

[a] $p = .005$ for significant age effects with chi-square test.

[b] $p = .006$ for significant age effects with chi-square test.

[c] Average $F_{st} = .050$ for the variable loci (Table 6.1) measures differentiation due to age; $p \leq .05$ for significant age effects for both loci with chi-square test.

Pond during the same two years, with a highly significant difference in allele frequencies observed between years (mean $F_{st} = .048$ and .065, respectively). These F_{st} values were calculated without including data from recaptured animals in 1984. Thus, processes within populations result in intrapopulational variances as great as the variance among populations on the SRP. The temporal differences in allele frequencies observed between years in Pond B suggest that the population showed significant evolutionary change over this year, probably because of recruitment of young or the effects of immigrants on the breeding structure. Demographic processes may be equally important to both inter- and intrapopulational differentiation.

The data from Lost Lake and Steed Pond in 1983 and 1984 provide further evidence of disequilibrium. During the first year, the populations exhibited significant deviation in expected Hardy-Weinberg genotypic proportions for three of six variable loci at one location and for three of six loci at the second location. These deviations were not observed in the second year. This difference may be the result of habitat loss, dispersal, and subsequent reproduction among turtles that had previously occupied different locations. In 1981 a large number of turtles from the peripheral ponds moved into the Lost Lake System because of a severe drought in the area. Turtles collected during 1983 exhibited significant deviations from Hardy-Weinberg equilibrium, all in the direction of heterozygote deficiencies, which would be predicted if turtles from populations with differing allele frequencies had been combined in one sample (Wahlund Effect; Wahlund, 1928). The second year's sampling included 2- and 3-year-old turtles that were produced during the drought. The populations were all in Hardy-Weinberg equilibrium during this second year because of the recruitment of these two cohorts.

During droughts, turtles probably move to areas with permanent water and remain there until favorable conditions reoccur (Gibbons et al., 1983). The relatively rapid reestablishment of equilibrium suggests that many of the 1983 immigrants emigrated from the Lost Lake System in 1984. Similar movements were probably occurring at Pond B, because the changes there also took place during and after the drought. Even though turtles often occur in discontinuous habitats, their populations are highly dynamic, and animals are interchanged, especially during periods of habitat loss.

Although turtles are known to make frequent movements between populations (Morreale et al., 1984; Parker, 1984), the genetic data show that these populations have different allele frequencies at a number of loci. One way to explain this seeming contradiction is to assume that the dispersers are not a random genetic subset of the turtles that are in these populations (Brown, 1985). The latter phenomenon can alter the conclusion that large amounts of dispersal cause allele frequencies to be essentially the same through space. However, there is no evidence that nonrandom dispersal by genotype occurs in turtles, so other factors are probably involved in explaining the spatial heterogeneity of allele frequency in *T. scripta*.

Low effective population size (N_e) is usually implicated as a principle cause of stochastic changes in allele frequency (Wright, 1969, 1970). Effective population size is a function of the number of individuals that actually contribute reproductively to the next generation (Crow and Kimura, 1970), and such things as sex ratio and variability in reproductive output can dramatically reduce N_e. Many turtles may breed, but if their offspring do not survive to the next generation for some reason, even chance, then they are not a part of the effective breeding population. The actual situation for breeding turtles may involve high variance in reproductive output because predators often eliminate entire clutches from some females (Congdon et al., 1983b). In any one year the eggs of a relatively small proportion of the adult females may survive. It could be a matter of chance that predators find some eggs and not others. Stochastic change is possible when a small number of a surviving cohort eventually breed and dis-

proportionately influence the allele frequency and heterozygosity of the population. Under such circumstances a population could be different from adjacent ones for a number of years before dispersal and reproduction eliminated or greatly reduced the interpopulational genetic differences. The high heterozygosity of *T. scripta* indicates that low N_e is not expected as a general rule but could periodically occur.

Selection could also be involved in determining some of the genetic differences within and among populations. Selection is difficult to prove in natural populations, but some of the data for *T. scripta* suggest its effect. Two-, 3-, and 4-year-old turtles are significantly less heterozygous than older turtles in Pond B, a stable reservoir that supports a large turtle population. The Pond B population should be more resistant to chance fluctuations and be in approximate equilibrium with all subgroups having similar genetic characteristics. The source and mechanism for the selection are not known, but two other vertebrates on the SRP show similar changes in *H* (Smith and Chesser, 1981; Cothran et al., 1983), and there are a number of vertebrates that show age- or size-related changes in allele frequencies (e.g., Tinkle and Selander, 1973; Feder et al., 1984; Chesser and Smith, 1987). If additional sampling shows size- or age-related genetic changes to be common and their pattern of change similar across a series of turtle populations, then selection associated with some life history trait would be strongly suggested. The lower *H* in the young classes in Pond B is opposite of that expected if dispersal and subsequent reproduction are the cause of the age-related differences.

Regardless of whether the changes in the frequencies of the genetic characteristics are brought about stochastically or in a deterministic manner, there are consequences for the genetic quality of the offspring of turtles that are dispersing among genetically different populations. When allele frequencies differ significantly at a number of loci, as appears to be the case for *T. scripta* (Table 6.2), dispersing individuals are likely to breed with others that have different alleles in their genome. The offspring from matings involving a disperser and a resident are likely to be more heterozygous than those from matings between two residents in the same population. The latter type of mating probably involves more inbreeding than matings involving a disperser. Inbreeding is not necessarily detrimental (Shields, 1982), but it does change *H*, which is correlated with a number of functional traits in vertebrates (Mitton and Grant, 1984). As the ratio of inbred and outbred matings and/or the ratio of highly heterozygous and less heterozygous turtles in the population change, the functional properties of the populations are also likely to change (Smith et al., 1978). The result is the same if turtles from a population's subgroups have significantly different allele frequencies and breed with one another. These subgroups might be composed of animals of different cohorts, ages, or sexes.

For our purposes many of the correlates of *H* are components of, or have direct effects on, secondary productivity. The best-studied animal in this regard is the white-tailed deer on the SRP. Antler growth and number of spikes both increase in the most heterozygous males (Smith et al., 1982; Scribner et al., 1984b; Scribner and Smith, n.d.). The most heterozygous females are the largest within each age class, have faster-growing fetuses, breed later in the season (Cothran et al., 1983), tend to have twins rather than single offspring (Chesser and Smith, 1987), have higher levels of body fat prior to conception, and lose body fat at slower rates during pregnancy (Cothran et al., 1987). Other vertebrates also show changes in reproductive rate, growth rate, and/or body size correlated with increasing *H* (Smith et al., 1975; Smith and Chesser, 1981; King, 1985). Basal metabolism and morphological asymmetry are also correlated with *H* in amphibians and reptiles (Mitton and Grant, 1984). The changes in heterozygosity with age in the Pond B turtles (Table 6.3) might also be due to a correlation with body size, which also increases with age. However, sample size will need to be increased to reliably separate the effects of age and body size on *H*. Heterozygosity-correlated changes in secondary productivity might be expected in all vertebrates if the cause is decreased maintenance metabolism in the most heterozygous animals (Garton et al., 1984). If energy intake is the same in animals of differing heterozygosities, then the most heterozygous ones would have more energy for growth and reproduction.

If size does change as a function of *H*, then size would have a profound effect on the number of eggs laid by breeding females and probably the reproductive rate of the local populations. Body size is the most important correlate of clutch size within a species of turtle (Gibbons, 1982; Congdon and Gibbons, 1983, 1985). Thus, the interaction of genetically different populations could alter the heterozygosity of resulting offspring and their reproductive contribution to these populations. A small difference in female body size of 10% to 20% within an age class could result in a much larger impact on the numbers of turtles in a population. The potential impact of genetics on the demography of turtles has yet to be studied, but density is correlated to *H* in old-field mice (Smith et al., 1975). Studies on the effects of genetic variability on the density and demography of *T. scripta* are needed.

In summary, populations of *T. scripta* are not genetically homogeneous over the SRP, over years, or among demographic units. The amount of heterogeneity in allele frequency due to demography within a single population is as great as that among turtles from the 16 locations on the SRP. The overall amount of heterogeneity is especially

surprising, considering the relatively small distances and short time periods considered in this study. In addition, gene flow appears to be relatively high and might be expected to result in homogeneous allele frequencies among populations. The results of stochastic processes might be amplified through population expansion or differential reproductive success of certain turtles, and reversal of the resulting genetic disequilibrium through gene flow might take many generations. Thus, dispersal, stochastic events, and natural selection may all be interacting to produce a series of populations that are in a state of dynamic disequilibrium, which can be dramatically affected by environmental conditions such as droughts.

Trachemys scripta presents an interesting situation in which to study the interaction of these processes, and the effects observed in this study may be occurring generally in many vertebrates with a shorter life cycle, which results in more opportunities for rapid genetic changes. These short-term evolutionary changes could have direct effects on population processes by altering the functional properties of individuals. The importance of genetics, environmental factors, and their interactions to population dynamics of *T. scripta* needs to be evaluated within a regional context to obtain an understanding of changes or differences in density within and among populations.

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