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EFFECTS OF POSTGLACIAL RANGE EXPANSION ON ALLOZYME AND QUANTITATIVE GENETIC VARIATION OF THE PITCHER-PLANT MOSQUITO, *WYEOMYIA SMITHII*

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Abstract.—We determined allozyme variability of 34 populations of the pitcher-plant mosquito, *Wyeomyia smithii*, from Florida (30°N) to northern Manitoba (54°N) and compared allozyme variability with the additive genetic variance for preadult development time and photoperiodic response determined previously for six populations over a similar range (30–50°N). Phylogenetic analysis of allozymes shows a well-defined split between Gulf Coast and lowland North Carolina populations, similar to previously observed phylogeographic patterns in a wide variety of taxa. A deeper split in the phylogeny of *W. smithii* coincides with the location of the maximum extent of the Laurentide Ice Sheet. Furthermore, both average heterozygosity and patterns of isolation-by-distance decline in populations north of the former glacial border. It is likely that northern populations are the result of a range expansion that occurred subsequent to the late-Wisconsin retreat of the Laurentide Ice Sheet and that these populations have not yet reached a drift-migration equilibrium. The northern decline in allozyme heterozygosity contrasts sharply with the northern increase in additive genetic variance of development time and photoperiodic response found in previous studies. These previous studies also showed that the genetic divergence of populations has involved stochastic variation in the contribution of dominance and epistasis to the genetic architecture underlying demographic traits, including preadult development time, and photoperiodic response. When taken together, the present and prior studies identify the genetic processes underlying the lack of concordance between geographic patterns of allozyme and quantitative genetic variation in natural populations of *W. smithii*. In the presence of nonadditive genetic variation, isolation and drift can result in opposite patterns of genetic variation for structural genes and quantitative traits.

Key words.—Founder event, genetic architecture, genetic drift, genetic variation, heterozygosity, isolation-by-distance, mosquito systematics, *Wyeomyia smithii*.

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Describing patterns of within- and between-population genetic variability and understanding the forces that shape the observed patterns has been a primary focus of evolutionary studies over the last 50 years (Fisher and Ford 1947; Dobzhansky 1951; Mayr 1954, 1963; Fisher 1958; Wright 1978; Schemske 1984). However, inferring processes of evolutionary change from extant patterns of variation has often been difficult. In part, this difficulty arises from the fact that population-structure data based on protein gel electrophoresis and DNA sequencing rarely can be combined with information on historical biogeography and life-history evolution to provide insight into the relationship between evolution at the molecular and phenotypic levels.

Extensive knowledge of the evolutionary ecology of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), provides a unique opportunity to examine the evolutionary dynamics of structural gene loci and quantitative characters. Previous studies with *W. smithii* have documented stochastic variation in the contribution of nonadditive genetic variation (i.e., dominance and epistasis) to the genetic architecture underlying both demographic traits, including preadult development time (Armbruster et al. 1997), and photoperiodic response (Hard et al. 1992, 1993; Lair et al. 1997). Furthermore, the additive genetic variance of both preadult development time and photoperiodic response increases with increasing latitude, paralleling the historical range expansion of *W. smithii* in North America (Hard et al. 1993; Bradshaw et al. 1997). Most studies assume that levels of variation at structural gene loci will

reflect variation for quantitative characters. We now seek to examine this assumption by comparing geographic patterns in genetic variation of quantitative traits with genetic variation for structural genes.

In this study, we survey allozyme variability at 10 loci within and among 34 populations of the pitcher-plant mosquito, *W. smithii*. We examine phylogeographic structure, patterns of isolation-by-distance, and latitudinal variation in population heterozygosity. We then compare results derived from allozymes to known patterns of phenotypic evolution and quantitative genetic variability to make inferences regarding causality for disparate geographic patterns in genetic variation underlying quantitative traits and structural genes.

Wyeomyia smithii

Adult *W. smithii* lay their eggs exclusively within the water-filled leaves of the carnivorous purple pitcher plant, *Sarracenia purpurea* L., wherein preadult development takes place utilizing decomposing prey and microbes within the leaves of the host plant. The geographical distribution of *W. smithii* follows that of its host plant from the Gulf of Mexico north to Labrador and west to Saskatchewan. Throughout their range, *W. smithii* overwinter as aquatic larvae in the leaves of *S. purpurea* in a state of developmental arrest (diapause) whose onset, maintenance, and termination are regulated by photoperiod. The critical photoperiod for the initiation and termination of diapause increases with both latitude and altitude throughout the range of *W. smithii* ($R^2 = 0.96$; Bradshaw 1976), representing a crucial local adaptation along the seasonal climatic gradient of North America.

Wyeomyia smithii is the sole temperate species of a large

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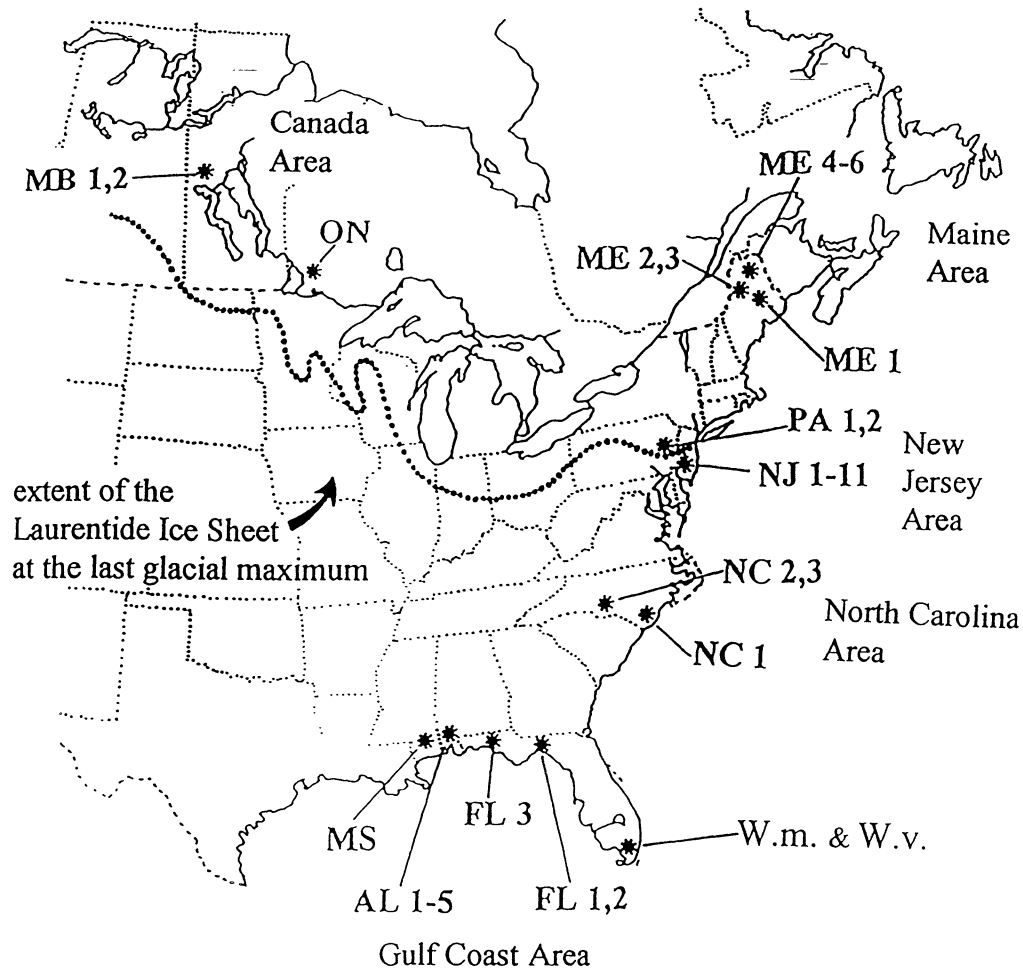


FIG. 1. Geographic origin of populations of *Wyeomyia smithii* sampled for allozyme analysis. Locality labels are state or province postal-code abbreviations followed by numerical designation for each population. Five local areas are defined as follows: Gulf Coast area at 30–31°N (FL 1–3, AL 1–5, MS); North Carolina area at 34–35°N (NC 1–3); New Jersey area at 40–42°N (NJ 1–11, PA 1–2); Maine area at 45–46°N (ME 1–6); and Canada area at 50–54°N (ON, MB 1–2). The maximum extent of the Laurentide Ice Sheet at approximately 21,000 yr. B.P. is shown by the dashed line and defines the boundary between the southern and northern regions of *W. smithii*'s distribution. W.m. & W.v., collection sites for *W. mitchelli* and *W. vanduzeei*.

neotropical genus (Lane 1953; Stone et al. 1959). Disparate populations of *W. smithii* form fertile hybrids in the laboratory. In hybrids between northern (Maine, Ontario) and southern (eastern Florida, western Florida) populations, there is heterosis in the F_1 and mild outbreeding depression in the F_2 under near-optimal conditions and heterosis in both the F_1 and F_2 under stressful conditions (Armbruster et al. 1997). The F_1 hybrids between northern and southern populations show intermediate morphological and physiological phenotypes that are indistinguishable from the phenotypes of geographically intermediate populations (Bradshaw and Lounibos 1977). Therefore, *W. smithii*'s geographic distribution, morphology, physiology, and reproductive biology all argue that *W. smithii* is a single species of mosquito that has invaded North America from South America and has subsequently undergone diversifying evolution from south to north (Ross 1964; Bradshaw and Lounibos 1977; Istock and Weisburg 1987; Bradshaw and Holzapfel 1990).

MATERIALS AND METHODS

Diapausing larvae were collected from 34 populations spanning nearly the entire distribution of *W. smithii* (Fig. 1). Sampling was designed to assess both local and regional patterns of allozyme variability. Thus, for the purposes of this study, we define five local areas as follows: (1) the Gulf Coast area, including populations in Florida, Alabama, and Mississippi; (2) the North Carolina area; (3) the New Jersey area, including populations in New Jersey and Pennsylvania; (4) the Maine area; and (5) the Canada area, including populations from Ontario and Manitoba. Populations from the Gulf Coast, lowland North Carolina, and New Jersey areas comprise the southern region of *W. smithii*'s distribution and populations from New Jersey northward constitute the northern region of the species' distribution.

The leaves of at least 20 plants were sampled from throughout each bog/pine savannah (i.e., population). The bog was previously shown to be the scale at which panmixia occurs

in *W. smithii* (Istock and Weisburg 1987). All collections were made in the spring before adult emergence, when 100% of the population was confined to pitcher-plant leaves as overwintering larvae. Hence, 100% of the genotypes in the population were available as larvae for sampling. Live larvae were transported to the laboratory, grown to adulthood, and frozen at -80°C so that genotypic samples were obtained directly from populations overwintering in the wild. Collections of *Wyeomyia mitchelli* and *W. vanduzeei*, bromeliad-breeding mosquitoes in subtropical Florida, were taken from southern Everglades National Park (Fig. 1) to be used as outgroups in the phylogenetic analysis.

Horizontal starch gel electrophoresis was performed for 10 allozyme loci using standard techniques (Steiner and Joslyn 1979). The gels consisted of 35 g hydrolyzed potato starch (Starch Art Co., Smithville, TX) in 350-ml buffer. Adenylate kinase (*Ak*: E.C. 2.7.4.3) and malic enzyme (*Me*: E.C. 1.1.1.40) were run on the Ca-8 buffer system, two isocitrate dehydrogenase loci (*Idh-1*, *Idh-2*: E.C. 1.1.1.42) and α -glycerophosphate dehydrogenase (α -*Gpdh*: E.C. 1.1.1.8) were run on the Ca-7 buffer system. Phosphoglucosmutase (*Pgm*: E.C. 2.7.5.1), phosphoglucose isomerase (*Pgi*: E.C. 5.3.1.9), aldehyde oxidase (*Ao*: E.C. 1.2.3.1), and two hexokinase loci (*Hk-2*, *Hk-4*: E.C. 2.7.1.1) were stained as described in Steiner and Joslyn (1979), but with the gel and running buffers of Lynch (1983). Comparison of electromorph band position was made by running different populations on the same gel. Between 50 and 70 individuals from each population were scored at each locus.

Genotypic frequencies were tested against Hardy-Weinberg expectations with log-likelihood ratio tests. For each population, Nei's (1987) average gene diversity (H) was computed as the expected heterozygosity averaged across all loci. The computed H was arcsine-square-root transformed to conform to the assumptions of least-squares regression (Zar 1984), and the transformed value was used to examine the relationship of H to latitude.

Nei's (1975) G_{ST} was calculated as $G_{ST} = (H_t - H_s)/H_t$, where H_t is the total population heterozygosity and H_s is the average within-population heterozygosity. We chose G_{ST} , the multiallelic/multilocus form of Wright's familiar F_{ST} , because it provides a measure of population differentiation that is robust to variation in number of alleles and mutation rate among loci (Crow 1986).

The geographic distance between populations was computed in ARC/INFO (1992), using an Albers projection, as the straight-line distance between points of latitude and longitude that were estimated to the nearest minute for all U.S. population locations from Map Expert (1993). The latitudes and longitudes for populations in Canada were estimated from 1:50,000 topographical maps from the Surveys and Mapping Branch, Department of Mines and Resources, Canada.

To test for regional patterns of isolation-by-distance, we performed regressions of G_{ST} for population pairs on geographic distance between populations. A significant positive slope of G_{ST} against geographic distance implies a pattern of isolation-by-distance. Because the points in these regressions represent populations pairs that are not independent, significance cannot be assessed using standard parametric

approaches. Therefore, consistent with previous analyses of this type of data (Preziosi and Fairbairn 1992; Britten et al. 1995), Mantel's randomization test was employed to evaluate the significance of these regressions (Manly 1991). Five thousand randomizations were performed for each test to evaluate the null hypothesis of no pattern of isolation-by-distance. Tests for isolation-by-distance were performed for the southern and northern regions.

To compare patterns of isolation-by-distance between the southern and northern regions, we tested for a difference in the slope of the regression of G_{ST} on geographic distance. Although the slope of the regression is not biased by the nonindependence of points, the standard error of the slope is biased. A simple and conservative approach to this problem was to calculate the standard error of the slope by determining the degrees of freedom from the number of populations in each regression instead of the number of points in the regression (i.e., population pairs). Comparison of slopes was made using a t -test (Zar 1984), and degrees of freedom were again determined using the number of populations in each regression.

Phylogenetic analysis was performed using Felsenstein's (1995) PHYLIP package (vers. 3.55). Nei's (1975) genetic distance (D) was computed and used to construct a UPGMA phenogram. We used Nei's genetic distance because fixed differences at two loci between local areas suggested that mutation had contributed to the divergence between populations in this study. A bootstrap analysis was performed by resampling the gene frequency data, calculating the corresponding genetic distance matrices among populations, and then building the consensus UPGMA tree (Felsenstein 1995).

Detailed procedures for measuring the additive genetic variances of critical photoperiod and development time are given in previous papers (Hard et al 1993; Bradshaw et al. 1997). The additive genetic variance of critical photoperiod was estimated by parent-offspring regression (Hard et al. 1993). The additive genetic variance of development time was estimated from the direct response of this trait to six generations of divergent selection (Bradshaw et al. 1997).

RESULTS

Banding patterns for all loci conformed to the expectations of enzyme structure (Steiner and Joslyn 1979). Of the 10 loci assayed, five were polymorphic (frequency ≥ 0.05) within at least 16 of 34 populations: *Ak*, *Ao*, *Hk-4*, *Pgm*, and *Pgi*. Alleles at each of the other five loci varied among populations. There were fixed differences between the Gulf Coast area and populations from New Jersey northward at two loci, *Hk-2* and *Idh-1*. A summary of the average allozyme frequencies and the average gene diversity within each of the five areas is presented in Table 1.

Seven of the 123 tests for deviation from Hardy-Weinberg expectations were significant at the $P = 0.05$, but not the $P = 0.01$ level. Of 123 tests, six would be expected to be significant at the $P = 0.05$ level by chance alone and no test was scored as significant using the sequential Bonferroni method (Rice 1989). There was no clear pattern of heterozygote excess or deficiency and no relationship between geographic location and deviation from Hardy-Weinberg expect-

TABLE 1. Average allozyme frequencies and average gene diversity (*H*) for each of the five local areas sampled.

Area	Ak*	Ao	α -Gpdh	Hk-2	Hk-4	Idh-1	Idh-2	Me	Pgi	Pgm	H
Gulf Coast	F+ < 0.01**	F = 0.02	M = 0.98	F = 1.00	M = 1.00	S = 1.00	F+ < 0.01	F = 0.01	F+ < 0.01	F++ < 0.01	0.17
	F = 0.54	M+ < 0.01	S = 0.02				F = 0.01	M+ < 0.01	F = 0.66	F = 0.23	
	M = 0.45	M = 0.94	S- < 0.01				M = 0.97	M = 0.95	M = 0.34	M = 0.66	
	S = 0.01	S = 0.04				S = 0.01	S = 0.01	S = 0.04	S < 0.01	S = 0.11	
						S- < 0.01					
North Carolina	M = 0.99	M = 1.00	F < 0.01	F = 0.80	M = 0.61	S = 1.00	F+ < 0.01	F < 0.01	F+ < 0.01	F+ = 0.01	0.18
	S < 0.01		M = 0.99	M = 0.20	S = 0.39		M = 0.99	M = 0.96	F = 0.32	F = 0.26	
							S = 0.01	S = 0.04	M = 0.68	M = 0.64	
										S = 0.07	
										S- = 0.02	
New Jersey	F = 0.05	F = 0.03	F < 0.01	S = 1.00	F = 0.54	F = 1.00	F+ = 0.01	F < 0.01	F+ = 0.01	F++ = 0.01	0.16
	M = 0.93	M = 0.96	M = 0.99		M = 0.46		F = 0.02	M = 0.99	M = 0.98	F+ = 0.09	
	S = 0.02	S = 0.01	M- < 0.01				M = 0.95	S = 0.01	S = 0.01	F = 0.02	
		S < 0.01				M- < 0.01	S = 0.02			M = 0.42	
										S = 0.46	
Maine	M = 0.99	M = 0.90	M = 0.99	S = 1.00	F = 0.29	F = 1.00	M = 1.00	M = 0.98	F+ = 0.04	F+ = 0.03	0.13
	S < 0.01	S = 0.10	S < 0.01		M = 0.71			S = 0.02	M = 0.93	F = 0.06	
									S = 0.03	M = 0.46	
Canada	M = 0.98	M = 0.71	M = 0.99	S = 1.00	F = 0.04	F = 1.00	M = 1.00	M = 1.00	F < 0.01	F < 0.01	0.10
	S = 0.02	S = 0.29	S < 0.01		M = 0.96				M = 0.99	M = 0.59	
									M- < 0.01	S = 0.41	

* Locus labels as described in Materials and Methods.

** Allele labels denote relative mobility: F, fast; M, medium; S, slow; +, fast; -, slow; F+, faster than F; S-, slower than S.

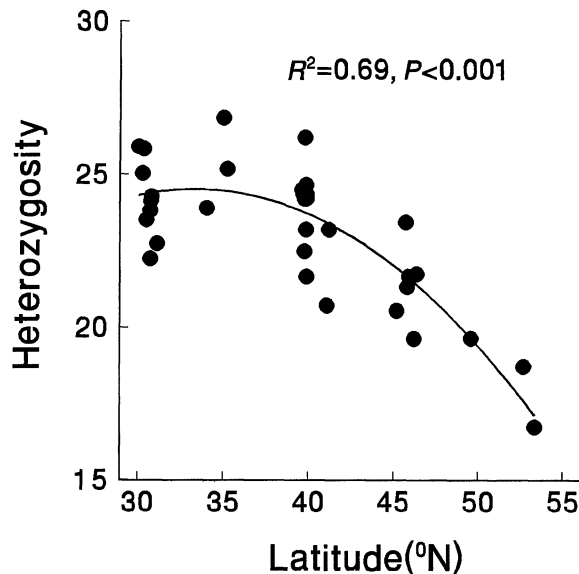


FIG. 2. Relationship between average heterozygosity (arcsine-square-root transformed) at 10 allozyme loci and latitude in 34 populations of *Wyeomyia smithii*.

tations (three deviations in Gulf Coast, two deviations in New Jersey, two deviations in Maine). We therefore concluded that the dataset as a whole did not depart significantly from Hardy-Weinberg expectations.

Nei's average gene diversity (H) ranged from a high of 0.203 in a North Carolina population to a low of 0.087 in a Manitoba population. The quadratic regression of average gene diversity on latitude was highly significant ($R^2 = 0.69$, $P < 0.001$; Fig. 2). Average gene diversity within populations remained relatively constant from the Gulf Coast to New Jersey (30–40°N) and declined dramatically north of New Jersey.

In our comparison of isolation-by-distance between the southern and northern regions we included the New Jersey populations in both regions (Fig. 3). Including the New Jersey populations in the southern region shows effects of divergence up to the northernmost region during the maximum extent of the Laurentide Ice Sheet; including them in the northern region shows the effects of northward dispersal since the recession of the Laurentide Ice Sheet. G_{ST} was positively correlated with geographic distance in both the southern ($R^2 = 0.87$, $P < 0.001$) and northern ($R^2 = 0.60$, $P < 0.001$) regions (Fig. 3). Regression of G_{ST} on distance was steeper in the southern than in the northern region ($t = 121.67$, $P < 0.001$).

A UPGMA phenogram based on Nei's genetic distance (Fig. 4) shows that *W. mitchelli* clusters more closely to the *W. smithii* group than does *W. vanduzeei*. This result is consistent with morphological differences among these three species (Darsie and Ward 1981). Within *W. smithii*, a deep split separating the Gulf Coast and North Carolina populations from the New Jersey and more northern populations is consistent with fixed differences at two loci (*Hk-2*, *Idh-1*) between these areas. Figure 4 also shows a well-defined split between the Gulf Coast and North Carolina populations. This clustering therefore shows strong phylogeographic structure

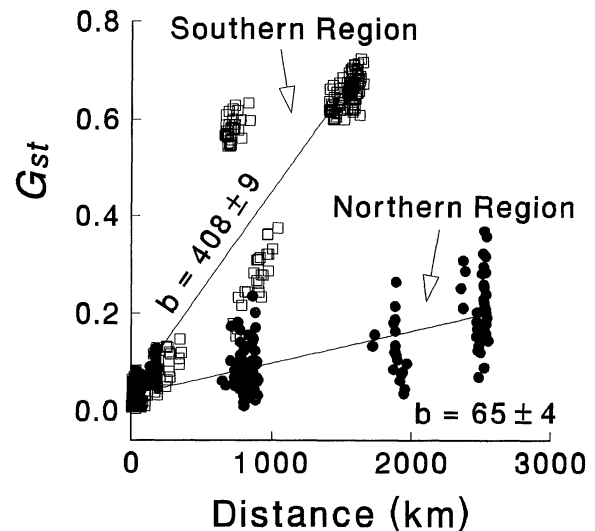


FIG. 3. Regional patterns of isolation-by-distance in *Wyeomyia smithii*. The southern region includes populations from the Gulf Coast, North Carolina, and New Jersey areas; the northern region includes populations from the New Jersey, Maine, and Canada areas. The four discrete clusters of points in the southern region represent differentiation (1) within areas; (2) between Gulf Coast and North Carolina populations; (3) between North Carolina and New Jersey populations; and (4) between Gulf Coast and New Jersey populations. The four discrete clusters of points in the northern region represent divergence (1) within areas; (2) between New Jersey and Maine populations; (3) between Maine and Canadian populations; and (4) between New Jersey and Canadian populations. The slopes of the regression lines in each region are shown as ($b \pm 1 \text{ SE}$) $\times 10^6$.

from the Gulf Coast to New Jersey and low levels of differentiation among populations from New Jersey northward. These results parallel the isolation-by-distance data (Fig. 3), which show discrete clustering among areas in the southern region of *W. smithii* and more diffuse clustering among populations in the northern region.

DISCUSSION

Wyeomyia is a large neotropical genus with only two subtropical species, *W. mitchelli* and *W. vanduzeei*, and only one temperate species, *W. smithii*, that extends from the Gulf of Mexico to Canada (Lane 1953; Stone et al. 1959; Darsie and Ward 1981). Like most mosquitoes, larval *W. smithii* from the Gulf Coast possess four long anal papillae; coastal and Piedmont North Carolina populations possess two long ventral and two short dorsal papillae; all more northern populations possess but two moderately lengthened ventral papillae (Bradshaw and Lounibos 1977). Gulf Coast and lowland North Carolina populations are obligately nonbiting for the first ovarian cycle, but require a blood meal for the second and subsequent ovarian cycles. Northern females produce repeated egg batches without blood feeding, a highly unusual trait in mosquitoes without carnivorous larvae (Bradshaw 1980, 1986; O'Meara and Lounibos 1981; O'Meara et al. 1981). Gulf Coast populations diapause in the fourth instar; lowland North Carolina populations are polymorphic for third- or fourth-instar diapause; northern populations diapause in the third instar but may enter a second, fourth-instar

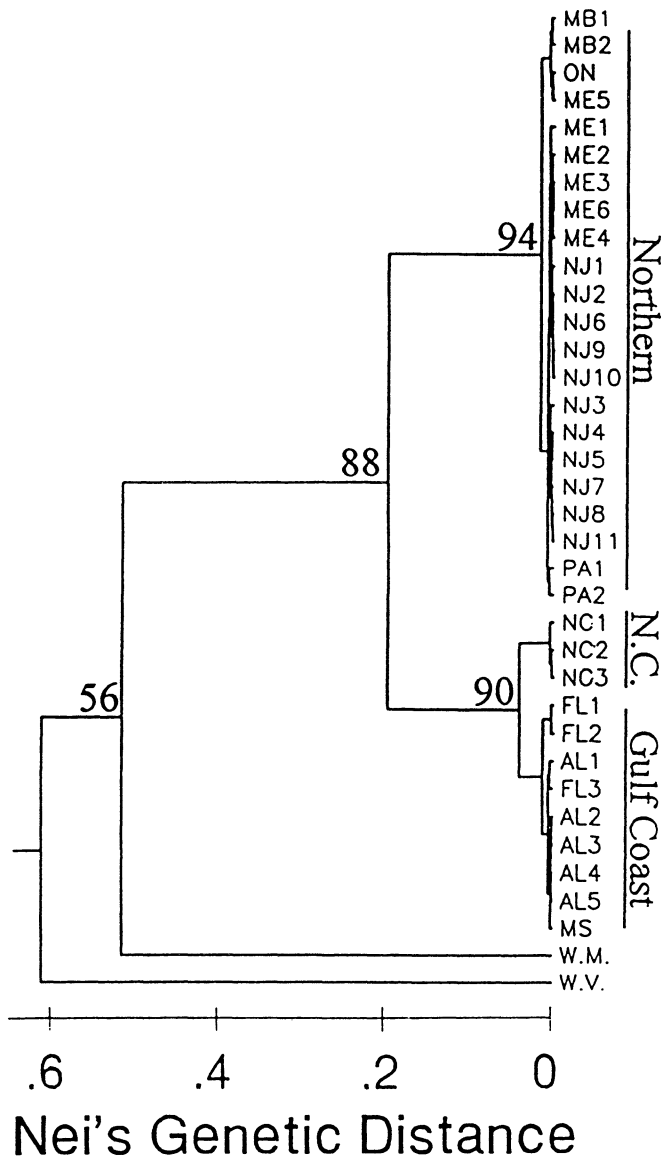


FIG. 4. UPGMA phenogram based on Nei's genetic distance. Bootstrap values at outer branches indicate the number of times a given clade was supported out of 100 resamplings of the gene frequency data (Felsenstein 1995). W.m. and W.v. represent *Wyeomyia mitchelli* and *W. vanduzeei*, respectively, which are subtropical species of bromeliad-breeding mosquitoes collected from peninsular Florida.

diapause (Lounibos and Bradshaw 1975; Bradshaw and Lounibos 1977). Thus, morphology of the anal papillae, diapause and reproductive physiology all distinguish the Gulf Coast, lowland North Carolina, and northern populations as distinct and separate groupings.

Phylogenetic analysis of allozyme variation among populations distinguishes the same geographic groupings (Fig. 4). First, there is a distinct split between the Gulf Coast and lowland North Carolina populations (bootstrap $P = 0.90$). Although little is known about the historical physical geography of the southeastern coastal plain, this split resembles patterns of mtDNA and allozyme variation found in a variety

of freshwater and marine fishes, as well as a number of terrestrial taxa surveyed by Avise and colleagues (Avise 1992). Second, there is an even deeper split between the southern clade, including the Gulf Coast and lowland North Carolina populations, and the more northern clade, including populations from New Jersey northward to Maine and westward to Manitoba (bootstrap $P = 0.88$). Paleoecological evidence indicates that pitcher plants, and presumably *W. smithii*, are likely to have survived the late-Wisconsin glaciation at the latitude of southern New Jersey and further south (Pielou 1991) and that these areas served as the source for the range expansion that occurred following deglaciation.

The maximum extent of the Laurentide Ice Sheet corresponds with a present-day break in the distribution of between-population variability between the southern and northern populations of *W. smithii*. Isolation-by-distance is strong from the Gulf Coast north to New Jersey but weakens from New Jersey northward (Fig. 3). The lower slope in the northern than in the southern region suggests that populations in the northern ($> 40^{\circ}\text{N}$) range of *W. smithii*'s distribution have not yet reached a drift-migration equilibrium (Slatkin 1993) since the retreat of the Laurentide Ice Sheet from this region over the last 8,000–21,000 years (Andrews 1987).

The maximum extent of the Laurentide Ice Sheet also defines a present-day boundary in the distribution of within-population variability between the southern and northern regions. Average heterozygosity is high and similar within populations in the southern region ($30\text{--}40^{\circ}\text{N}$), but declines north of 40°N latitude (Fig. 2). These results are similar to a number of studies that have reported an effect of late-Wisconsin Age ice sheets on allozyme heterozygosity (Highton and Webster 1976; Bellemin et al. 1978; Cwynar and MacDonald 1987; Boileau and Hebert 1991; Stone and Sunnuck 1993; Green et al. 1996), including *W. smithii*'s host plant, *S. purpurea* (Schwaegerle and Schaal 1979). *Wyeomyia smithii* is a small, weak-flying mosquito, highly prone to death by desiccation (Istock and Weisburg 1987). The mosquito's strict habitat requirements, in combination with the discrete distribution of its host plant, suggests that, in accordance with our allozyme data (Fig. 2), new populations are founded by a very small number of individuals or even a single inseminated female.

The steady decline in allozyme heterozygosity northward into the previously glaciated region of North America (Fig. 2) contrasts sharply with the increase in additive genetic variance for preadult development time and critical photoperiod for the maintenance of larval diapause in populations of *W. smithii* (Fig. 5). Although genetic drift is expected to decrease single-locus and purely additive genetic variance by the same amount (Wright 1969; Lande 1980), when nonadditive genetic variation (i.e., dominance and epistasis) affects quantitative characters, genetic drift can actually increase the additive genetic variance (Robertson 1952; Bryant et al. 1986; Goodnight 1987, 1988, 1995; Cockerham and Tachida 1988; López-Fanjul and Villaverde 1989; Willis and Orr 1993; Cheverud and Routman 1996). For particularly lucid explanations of this effect, see Goodnight (1987) and Willis and Orr (1993).

In fact, previous studies with *W. smithii* have demonstrated a substantial contribution of dominance and epistasis to the

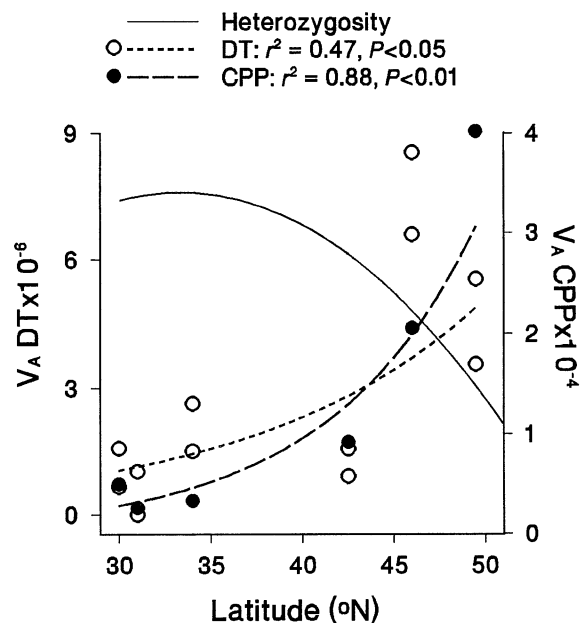


FIG. 5. Allozyme heterozygosity (Heterozygosity, Fig. 2) superimposed on additive genetic variance for preadult development time (DT: Bradshaw et al. 1997) and critical photoperiod (CPP: Hard et al. 1993) of *Wyeomyia smithii*. Both DT and CPP are fit to exponential functions.

divergence of the genetic architecture underlying both preadult development time (Armbruster et al. 1997) and photoperiodic response (Hard et al. 1992, 1993; Lair et al. 1997) between southern and northern populations. Therefore, the opposite trends in allozyme and quantitative trait variation in *W. smithii* can be explained by a release of additive from nonadditive variance due to the same isolation and drift that cause the decrease in allozyme variation. Although several laboratory experiments have documented such a process in experimentally manipulated lines (Bryant et al. 1986; López-Fanjul and Villaverde 1989), our results are the first to indicate that these effects actually occur in *natural populations*. These results provide an example of one mechanism that could underlie previous results in which allozyme variability has been a poor indicator of quantitative genetic variation (McCommas and Bryant 1990; Leary et al. 1992; Spitze 1993; Cheverud et al. 1994).

Prior studies with *W. smithii* argued on the basis of this mosquito's habitat specificity and biogeography that successive founder events were responsible for the stochastic variation in the contribution of dominance and epistasis to the divergence of demographic traits (Armbruster et al. 1997) and photoperiodic response (Hard et al. 1992, 1993; Lair et al. 1997) among populations. None of these studies, however, provided direct evidence that isolation and drift had been important in the northward genetic differentiation of *W. smithii* populations. The allozyme data in Figure 2 provides such evidence. When taken together, these studies identify the genetic processes underlying the lack of concordance between geographic patterns of allozyme and quantitative genetic variation in natural populations of *W. smithii*. In the presence of nonadditive genetic variation, isolation and drift can result

in opposite patterns of genetic variation for structural genes and quantitative traits (Fig. 5).

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