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THE GENETIC BASIS OF PHOTOPERIODISM AND ITS  
EVOLUTIONARY DIVERGENCE AMONG POPULATIONS  
OF THE PITCHER-PLANT MOSQUITO, *WYEOMYIA SMITHII*

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*Abstract.*—We measured the additive genetic variance within populations and the composite additive, dominance, and epistatic effects contributing to differentiation of photoperiodic response between two southern (ancestral) and each of four progressively more northern (derived) populations of the pitcher-plant mosquito, *Wyeomyia smithii*. Critical photoperiod and its additive genetic variance but not its heritability increased with latitude. Directional selection on critical photoperiod during the northward divergence of *W. smithii* has therefore not eroded the additive genetic variance underlying this trait. Joint scaling tests of crosses between populations showed that epistatic effects, especially additive  $\times$  additive and dominance  $\times$  dominance interactions, overwhelm composite additive and dominance effects on critical photoperiod. The presence of substantial epistasis suggests that multiple founder events during the northward divergence of *W. smithii* may have been responsible for the release of progressively greater additive genetic variance in derived populations, despite directional and stabilizing selection to reduce it. If epistasis makes a similar contribution to the genetic differentiation of populations in other species, then current models of adaptive evolution that consider only additive genetic variation and covariation within populations may be of limited value in predicting how natural populations differentiate in life history.

Identifying the genetic mechanisms underlying the adaptation and divergence of natural populations remains a fundamental evolutionary problem. Divergence is a product of mutation, genetic drift, natural selection, and dispersal, factors that can interact in complex ways to affect the evolution of quantitative characters. In Wright's (1977) shifting-balance theory, local adaptation and genetic divergence of populations depend on the interactive effects of drift and selection on genetic variation in quantitative characters. However, the roles that the different components of genetic variation play in this process remain elusive. While it has long been recognized that allelic and genic interactions (i.e., dominance and epistasis) may have important fitness consequences (Fisher 1958; Wright 1968, 1977), how these forms of nonadditive genetic variation affect adaptation and divergence is poorly understood. In the absence of sufficient genetic drift, the divergence of populations for traits with low additive genetic variance must involve the conversion of nonadditive to additive genetic variance, at least over the short term (see, e.g., Wade and McCauley 1984; Bryant et al. 1986b). Still, knowledge of the general importance of nonadditive genetic variation, especially epistasis, in the

evolution of quantitative characters affecting fitness is meager (Kearsey and Kojima 1967; Barker 1974, 1979; Hedrick et al. 1978; Gimelfarb 1989). Evidence for the relevance of this variation to the adaptation and divergence of populations is even less adequate (Bryant et al. 1986b; Cohan et al. 1989).

Interpreting the relationship between genetic variation and population differentiation is frequently hindered by a lack of knowledge about the evolutionary ecology of the organism in question. Two pieces of information, critical to the interpretation of this evolutionary relationship, are often unavailable. First, in many cases the characters under examination have little or unknown effects on fitness. Second, the evolutionary trajectory for a species (its major pattern of dispersal, colonization, and differentiation through time) is often unknown. As a result, little empirical work is available that relates potential evolutionary pathways of adaptation to actual patterns of differentiation. In this article, we take advantage of existing knowledge of an organism's evolutionary trajectory to examine genetic variation within and genetic differentiation among populations of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), for a trait that is both critical to fitness and correlated with a climatic gradient that parallels the evolutionary trajectory of the species. We then ask whether nonadditive genetic variation, particularly epistasis, is important in population differentiation under these conditions.

*Wyeomyia smithii* is distributed in eastern North America from the Gulf of Mexico (30°N) to north central Canada (54°N). Throughout its range, *W. smithii* completes its preadult development in the water-filled leaves of its host, the purple pitcher plant, *Sarracenia purpurea* L. The mosquitoes overwinter in the leaves in a larval diapause that is initiated, maintained, and terminated by photoperiod (Bradshaw and Lounibos 1977). Geographical, physiological, morphological, and behavioral evidence indicates that *W. smithii* has evolved from south to north in North America (Istock and Weisburg 1987; Bradshaw and Holzapfel 1990). Along this latitudinal gradient, the photoperiodic response of *W. smithii* to seasonal change in day length increases linearly with altitude and latitude ( $R^2 = 0.96$ ; Bradshaw 1976; Bradshaw and Lounibos 1977). Thus, the photoperiodic response of *W. smithii* reflects seasonal adaptation along its evolutionary trajectory in North America.

We define the critical photoperiod of an individual as the day length, under a regimen of increasing day length, at which an individual larva in short-day-maintained diapause (dormancy) responds to the increase in photoperiod and pupates (Hard et al. 1992). By extension, we define the critical photoperiod of a population as the mean of its individual critical photoperiods. Our basic experimental approach is first to estimate the additive genetic variance of critical photoperiod in six populations of *W. smithii*, two southern (30°N–31°N) and four progressively more northern (34°N–49°N), and then to make reciprocal crosses between the southern and northern populations establishing  $F_1$ ,  $F_2$ , and first back-cross hybrids. Finally, we determine the contribution of composite additive (independent effect of genes), dominance (allelic interaction), and digenic epistatic effects (interaction between pairs of loci) to the genetic divergence of the critical photoperiod of these populations.

TABLE 1  
ORIGINS AND GEOGRAPHICAL CHARACTERISTICS OF SAMPLED *WYEOMYIA SMITHII* POPULATIONS

Locality	Label*	Latitude (°N)	Longitude (°W)	Altitude (m)
FL1†	WI	30	85	10
FL2	CR	31	87	30
NC	GS	34	78	20
MA	FV	43	72	60
ME	KC	46	68	110
ON	DL	49	94	336

NOTE.—Locality designations are state or province postal abbreviations.

\* Label designations are as in Bradshaw and Holzapfel 1989.

† The location of FL1 is 300 km east of FL2.

#### METHODS

##### *Estimation of Additive Genetic Variance*

Approximately 2,000 overwintering *Wyeomyia smithii* larvae were collected from each of six localities in eastern North America, including Florida, North Carolina, Massachusetts, Maine, and Ontario (table 1). Mosquito populations were sampled in nature during the early spring when 100% of the population and, hence, of its genotypes, were restricted to larvae in pitcher-plant leaves. Maintenance of stock colonies and the basic experimental regimen were described in a previous article (Hard et al. 1992).

In order to eliminate residual cytoplasmic or maternal environmental effects from the field, the additive genetic variance of the critical photoperiod within each population was estimated after two generations of culture without artificial selection in the laboratory. First, heritability of critical photoperiod was estimated from parent-offspring regression after exposing parents and offspring to the same incrementing photoperiod as described in another article (Bradshaw and Holzapfel 1990), modified as follows. In the  $F_2$  generation, parental larvae in each population, diapausing in the same instar, were exposed to day lengths that were increased continuously 3 min/d, and they were examined daily for subsequent development. For each population, the resulting pupae for each 15-min increment in the photoperiod (equal to 5 d in real time) were combined into a parental cohort and placed in a cylindrical (250 mm high  $\times$  150 mm in diameter) screen cage, where the subsequent adults were allowed to mass swarm and oviposit. From six to nine such adult cohorts were created in each population. Their offspring ( $F_3$ ) were put on short days as eggs to induce diapause. Sixty days after the last  $F_3$  egg was oviposited, the diapausing larvae in each cohort were subjected to the same photoperiod regimen as that which their parents had experienced.

Combining pupae that eclosed over several days into cohorts was necessary to ensure sufficient mass swarming of adults because southern populations of *W. smithii* are reluctant to mate in the laboratory in single pairs. This procedure precluded knowledge of the photoperiods at development for individual parents; consequently, the analysis was based on mean photoperiods for parental cohorts.

Photoperiods were log transformed before calculation of means to reduce skewness, sexual dimorphism, and scaling of variances with means (Hard et al. 1992). The grouping of parents required the use of a grouping regression technique (Prais and Aitchison 1954; Haitovsky 1973) instead of simple linear regression to estimate the heritability of critical photoperiod. Grouping does not bias the slope of a regression so long as observations are grouped by values of the independent variable (the critical photoperiod of the parents), a procedure that minimizes within-group variation and maximizes between-group variation. Grouping does, however, inflate the correlation coefficient and consequently biases the variance of the slope downward relative to simple linear regression (Hannan and Burstein 1974). The maximum likelihood estimator for the grouped regression coefficient, which is based on Aitken's (1934) method of generalized least squares, was calculated from

$$\beta = [\bar{\mathbf{x}}^T(\mathbf{G}\mathbf{G}^T)^{-1}\bar{\mathbf{x}}]^{-1}\bar{\mathbf{x}}^T(\mathbf{G}\mathbf{G}^T)^{-1}\bar{\mathbf{y}}, \quad (1)$$

where  $\beta$  is the slope of the grouped regression (the point estimate of the narrow-sense heritability),  $\bar{\mathbf{x}}$  is the column vector of mean parental photoperiods in each cohort,  $\mathbf{G}$  is a grouping matrix corresponding to the one-way classification of parental photoperiods (Prais and Aitchison 1954), and  $\mathbf{y}$  is the column vector of mean offspring photoperiods resulting from each parental cohort (Haitovsky 1973). The elements of  $\bar{\mathbf{x}}$  and  $\bar{\mathbf{y}}$  are expressed as deviations from the unweighted generation means. The weighting matrix  $(\mathbf{G}\mathbf{G}^T)^{-1}$ , composed of  $\mathbf{G}$ , is a diagonal matrix whose elements are the number of parents contributing to each group and in which T denotes matrix transposition.

From generalized least squares, the estimator for the variance of  $\beta$  was calculated by

$$\text{Var}(\beta) = \sigma^2[\bar{\mathbf{x}}^T(\mathbf{G}\mathbf{G}^T)^{-1}\bar{\mathbf{x}}]^{-1}, \quad (2)$$

where  $\sigma^2$  is the error variance, estimated by

$$\sigma^2 = (\bar{\mathbf{y}} - \bar{\mathbf{x}}\beta)^T(\mathbf{G}\mathbf{G}^T)^{-1}(\bar{\mathbf{y}} - \bar{\mathbf{x}}\beta)/(m - p), \quad (3)$$

$m$  being the number of groups (parental cohorts) and  $p$  (equal to one) the number of independent (grouping) variables (Haitovsky 1973). The additive genetic variance of the critical photoperiod in each population was then calculated as the product of the heritability,  $\beta$  (already weighted by group size), and the total phenotypic variance (summed over all individuals in the population, regardless of group affinity). The 95% confidence limits of the additive genetic variance were calculated as the product of the total phenotypic variance and the upper or lower 95% confidence limit of the heritability. Absolute estimates of additive genetic variance based on these regressions may be biased upward, owing to assortative mating of parents (Gimelfarb 1985), but, because parental cohorts were established and estimates were made in all populations in the same way, the relative values of the variances should be unaffected.

#### *Contribution of Composite Genetic Effects to Divergence*

Mosquitoes used in the population crosses were obtained from the same populations as those used to estimate additive genetic variance of critical photoperiod,

but after 20 generations of culture without artificial selection in the laboratory. Minimum population size in each line during this period was approximately 150 individuals. If we assume the minimum population size of 150 for each generation and a 60:40 (male:female) realized sex ratio, the maximum cumulative inbreeding after 20 generations is 13.0% (Falconer 1981). Approximately 500 larvae were sampled from each line to initiate population crosses. In order to determine both the magnitudes of the composite genetic effects producing differences in critical photoperiod between populations of *W. smithii* and the pattern of effects along the latitudinal gradient, reciprocal crosses were made between each of the two southern (ancestral) populations (FL1, FL2) and each of the four progressively more northern (derived) populations (NC, MA, ME, and ON; table 1). Crosses included  $F_1$  and  $F_2$  hybrids and first backcrosses ( $B_1$  and  $B_2$ ), which yielded a total of 16 crosses and their derivatives (96 total lines). The establishment of crosses and the culture and assessment of their progeny were described in detail in an earlier article (Hard et al. 1992). For these crosses, between 32 and 62 adults of each sex were used to found parental control lines; between 73 and 106 of each sex were used to found  $F_1$  hybrids. For the  $F_2$  hybrids, between 25 and 89 of each sex were used to found each line, except in some crosses involving FL2 and NC, in which low offspring production in the  $F_1$  hybrid limited the numbers of parents to between 12 and 19 of each sex; the corresponding parental controls were limited to between 12 and 24 of each sex.

For each of the line-cross derivatives resulting from a pair of the parental populations, critical photoperiod and its standard error were determined from approximately 125 individuals under an increasing (3 min/d) photoperiod. The means of all lines, including parental controls, were transformed to deviations from the unweighted mean of the means of each replicated parental control.

Protandry in *W. smithii* resulted in a slight sexual dimorphism in critical photoperiod, and Mather's scaling tests A, B, and C (Mather and Jinks 1982, pp. 71–76) were all significantly negative, suggesting that a transformation that foreshortens the distribution was appropriate for these data. Transformation by  $\log_{10}$  reduced skewness, stabilized coefficients of variation, and eliminated any significant sexual dimorphism in critical photoperiod. Consequently, the data from males and females were pooled within a line.

After log transformation of individual critical photoperiods, the  $F_1$ ,  $F_2$ , and backcross hybrids of each reciprocal cross were first compared to test for maternal or cytoplasmic effects and sex linkage (Carson and Lande 1984). From line-cross theory (Cockerham 1980; Hill 1982; Mather and Jinks 1982; Lynch 1991), we then tested the means and variances of crosses for fit to genetic models, incorporating composite additive and additive-dominance effects with joint-scaling tests (Cavalli 1952; Hayman 1958, 1960a, 1960b) as described in our previous article (Hard et al. 1992). In brief, the critical photoperiods of the six lines (two parents,  $F_1$ ,  $F_2$ , and two backcrosses) resulting from crosses between any two parental populations were used to derive estimates of composite additive, dominance, and digenic epistatic effects for this trait. Goodness of fit of the line means to the additive-dominance model was tested with the  $\chi^2$  statistic derived by Hayman (1958). The level of significance used was  $P < .05$ . Acceptance of

the additive-dominance model indicates that additive and dominance effects alone are sufficient to explain the genetic divergence of critical photoperiod between the two populations. Rejection of the additive-dominance model indicates that epistasis and/or linkage are contributing to the genetic divergence of populations. In the presence of substantial epistasis, estimates of composite additive and dominance effects are unreliable (Hayman 1960*a*; Cockerham 1980). After rejection of the additive-dominance model, estimates of composite additive  $\times$  additive, additive  $\times$  dominance, and dominance  $\times$  dominance effects were obtained from the weighted least-squares estimates (Hayman 1958) with a six-parameter model. The adequacy of the six-parameter model was not, itself, tested for goodness of fit because the number of significant parameters usually equaled the number of observed lines, leaving no degrees of freedom (Hard et al. 1992).

Finally, the relationship between the composite genetic effects on divergence of critical photoperiod and the distance between populations along the latitudinal gradient was determined.

#### RESULTS

Critical photoperiod in the six populations of *Wyeomyia smithii* closely tracked latitude (fig. 1*A*). The heritability of critical photoperiod was not significantly correlated with latitude, despite an apparent increase in heritability in more northern populations (fig. 1*B*). By contrast, the estimate of additive genetic variance of critical photoperiod increased eightfold from the southernmost (30°N) to the northernmost (49°N) population sampled and showed an exponential rise with latitude (fig. 1*C*).

Comparison of reciprocal  $F_2$  and backcross hybrids yielded evidence for maternal or cytoplasmic effects on the divergence of critical photoperiod between some populations. Thirteen of the 24 reciprocal comparisons included means that differ significantly by a *t*-test (table 2). Of these 13 significant maternal or cytoplasmic effects, the critical photoperiod in crosses involving a northern female was higher in nine comparisons and that in crosses involving a southern female was higher in four of them, but this disparity was not significant (Fisher's exact test,  $P = .099$ ). The 13 significant maternal or cytoplasmic effects occurred in two (FL2-NC and FL2-MA) of the eight comparisons involving reciprocal  $F_2$  hybrids and 11 of the 16 comparisons involving reciprocal backcrosses, but, again, this disparity was not significant (Fisher's exact test,  $P = .110$ ). When significant maternal or cytoplasmic effects were indicated by both the reciprocal  $F_2$  hybrid and reciprocal backcrosses, the directional effect of the female on the critical photoperiod was consistent between the first backcross and  $F_2$  comparisons in one case but not the other. Thus, maternal or cytoplasmic effects occurred in about half the comparisons, but we could detect neither a geographical pattern nor any significant tendency of reciprocal  $F_2$  hybrids or reciprocal backcrosses to indicate maternal or cytoplasmic effects.

Comparison of reciprocal  $F_1$  males (Carson and Lande 1984) yielded no evidence for sex-linked effects on the divergence of critical photoperiod between populations, regardless of evidence for significant maternal or cytoplasmic effects

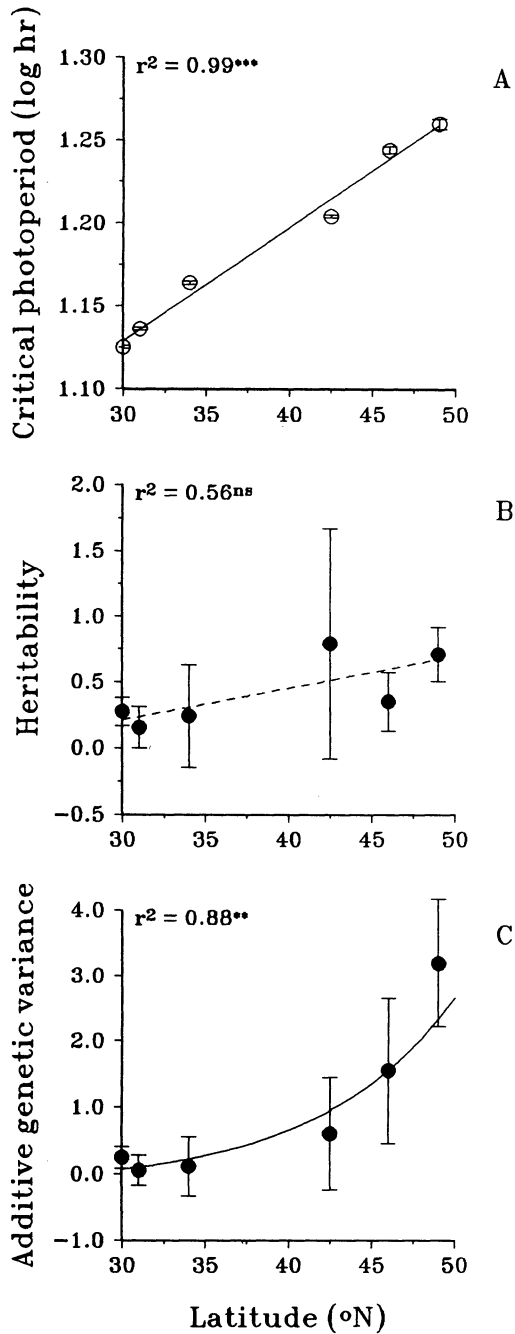


FIG. 1.—A, Increase in critical photoperiod (log h) in *Wyeomyia smithii* with latitude; B, relationship of heritability of critical photoperiod with latitude (LAT). The fitted equation is  $V_A = (6.75 \times 10^{-7}) (10^{0.054LAT})$ . All vertical bars are  $\pm 2$  SE; NS, not significant at  $P > .05$ ,  $** P < .01$ ,  $*** P < .001$ .



TABLE 2

TESTS FOR MATERNAL OR CYTOPLASMIC EFFECTS (RECIPROCAL BACKCROSSES AND RECIPROCAL F<sub>2</sub> HYBRIDS) AND SEX-LINKED EFFECTS (RECIPROCAL F<sub>1</sub> MALES) ON DIVERGENCE IN CRITICAL PHOTOPERIOD BETWEEN TWO SOUTHERN POPULATIONS (FL<sub>1</sub>, FL<sub>2</sub>) AND FOUR PROGRESSIVELY MORE NORTHERN POPULATIONS (NC, MA, ME, ON) OF *WYEMYIA SMITHII*

CROSS (♂ × ♀)	MATERNAL OR CYTOPLASMIC EFFECTS			SEX LINKAGE (F <sub>1</sub> ♂♂)
	F <sub>1</sub> ♀ × FL♂	F <sub>1</sub> ♀ × Northern ♂	F <sub>2</sub>	
FL <sub>1</sub> × NC	1.1209 ± .0015	1.1307 ± .0033	1.1238 ± .0016	1.1275 ± .0027
NC × FL <sub>1</sub>	1.1184 ± .0014 (126/124)*	1.1242 ± .0018 (137/128)***	1.1247 ± .0014 (132/146) <sup>a</sup>	1.1239 ± .0028 (58/58) <sup>a</sup>
FL <sub>1</sub> × MA	1.1384 ± .0020	1.1591 ± .0033	1.1538 ± .0020	1.1629 ± .0035
MA × FL <sub>1</sub>	1.1380 ± .0018 (119/136) <sup>a</sup>	1.1647 ± .0030 (97/116)*	1.1567 ± .0028 (141/131) <sup>a</sup>	1.1623 ± .0035 (55/68) <sup>a</sup>
FL <sub>1</sub> × ME	1.1603 ± .0029	1.2082 ± .0022	1.1770 ± .0039	1.1874 ± .0065
ME × FL <sub>1</sub>	1.1546 ± .0020 (130/143)**	1.2123 ± .0038 (113/130) <sup>a</sup>	1.1736 ± .0036 (128/111) <sup>a</sup>	1.1819 ± .0042 (37/55) <sup>a</sup>
FL <sub>1</sub> × ON	1.1537 ± .0020	1.1957 ± .0022	1.1686 ± .0024	1.1802 ± .0020
ON × FL <sub>1</sub>	1.1501 ± .0017 (143/127)**	1.1944 ± .0014 (130/133) <sup>a</sup>	1.1719 ± .0033 (133/143) <sup>a</sup>	1.1794 ± .0016 (73/85) <sup>a</sup>
FL <sub>2</sub> × NC	1.1246 ± .0024	1.1315 ± .0015	1.1304 ± .0013	1.1374 ± .0039
NC × FL <sub>2</sub>	1.1289 ± .0025 (119/117)*	1.1309 ± .0030 (121/147) <sup>a</sup>	1.1403 ± .0035 (121/123)***	1.1297 ± .0054 (31/58) <sup>a</sup>
FL <sub>2</sub> × MA	1.1449 ± .0025	1.1594 ± .0032	1.1643 ± .0028	1.1636 ± .0043
MA × FL <sub>2</sub>	1.1397 ± .0021 (141/136)**	1.1729 ± .0026 (97/109)***	1.1576 ± .0027 (138/124)***	1.1644 ± .0034 (76/62) <sup>a</sup>
FL <sub>2</sub> × ME	1.1663 ± .0020	1.2514 ± .0026	1.1831 ± .0029	1.1910 ± .0038
ME × FL <sub>2</sub>	1.1633 ± .0013 (112/132)**	1.2506 ± .0028 (128/116)***	1.1838 ± .0033 (121/124) <sup>a</sup>	1.1888 ± .0043 (65/58) <sup>a</sup>
FL <sub>2</sub> × ON	1.1509 ± .0018	1.1993 ± .0025	1.1700 ± .0027	1.1794 ± .0025
ON × FL <sub>2</sub>	1.1496 ± .0020 (145/131) <sup>a</sup>	1.1951 ± .0017 (120/133)**	1.1721 ± .0028 (143/119) <sup>a</sup>	1.1796 ± .0020 (57/66) <sup>a</sup>

NOTE.—Backcrosses are of reciprocal F<sub>1</sub> females crossed to the same parental line of males. Values are mean critical photoperiods (log h) ± 2 SE. Each pair of means is compared by *t*-test, whose significance is given after the corresponding sample sizes (in parentheses) directly below each comparison.

<sup>a</sup> *t*-Test is not significant at  $P > .05$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

in the corresponding F<sub>2</sub> hybrids or backcrosses (table 2). Reciprocal F<sub>1</sub> males did not differ significantly in any cross, which indicates that the contribution of sex-linked genes to divergence of critical photoperiod is unimportant. The differences between reciprocal F<sub>1</sub> males were less than half of the difference between the parental populations and usually less than 10% of this difference.

For all south-north crosses, joint scaling tests with a model incorporating only the combined composite additive and dominance effects were strongly rejected (range in  $\chi^2 = 68.9$ –1291.3, df = 3,  $P < .001$ ; fig. 2). This result means that at least digenic epistatic interactions have had substantial effects on the genetic divergence of critical photoperiod among populations. In order to test for the contribution of higher-order epistasis and/or linkage to divergence in the three of 16 crosses (ME ♂ × FL<sub>1</sub> ♀, ON ♂ × FL<sub>1</sub> ♀, and ON ♂ × FL<sub>2</sub> ♀) in which

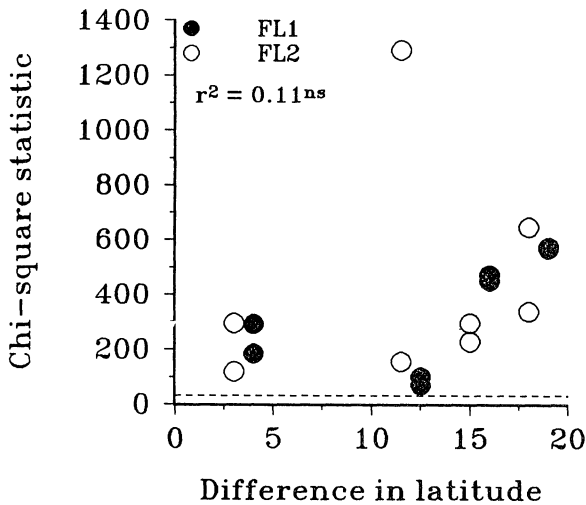


FIG. 2.—Results of joint scaling tests of line crosses testing lack of fit of the composite additive-dominance model. Significant values of  $\chi^2$  demonstrate inadequacy of additive and dominance effects alone and indicate progressively important contributions of linkage and epistasis to genetic divergence of critical photoperiod. The *dashed horizontal line* denotes the critical value of  $\chi^2$  for  $df = 3$  and  $P < .001$ .

TABLE 3

RESULTS OF JOINT SCALING TESTS FOR HIGHER-ORDER EPISTASIS AND/OR LINKAGE AFTER DROPPING NONSIGNIFICANT DIGENIC EPISTATIC TERMS FROM THE MODEL

Cross	Nonsignificant Interaction $\pm 2$ SE	Test for Linkage and/or Higher-Order Interactions <sup>a</sup>
ME $\delta \times$ FL1 $\phi$	D $\times$ D = .0110 $\pm$ .0190	17.94***
ON $\delta \times$ FL1 $\phi$	A $\times$ A = -.0024 $\pm$ .0134	.13 <sup>b</sup>
ON $\delta \times$ FL2 $\phi$	A $\times$ A = .0058 $\pm$ .0118	.95 <sup>b</sup>

NOTE.—The designations for epistasis are defined as follows: D  $\times$  D, dominance  $\times$  dominance epistasis; A  $\times$  A, additive  $\times$  additive epistasis.

<sup>a</sup>  $\chi^2$ ,  $df = 1$ .

<sup>b</sup> Not significant at  $P > .05$ .

\*\*\*  $P < .001$ .

nonsignificant digenic epistatic effects existed, the nonsignificant interaction terms were dropped from the additive-dominance model, as described in Mather and Jinks (1982, chap. 5) and in our earlier article (Hard et al. 1992). Evidence for higher-order epistasis and/or linkage was detected in the ME  $\delta \times$  FL1  $\phi$  cross; digenic epistasis was sufficient to explain divergence in the remaining two (table 3).

By contrast to additive genetic variance of critical photoperiod within populations, composite genetic effects contributing to the divergence of crossed populations showed no consistent geographical pattern. Neither total digenic epistasis

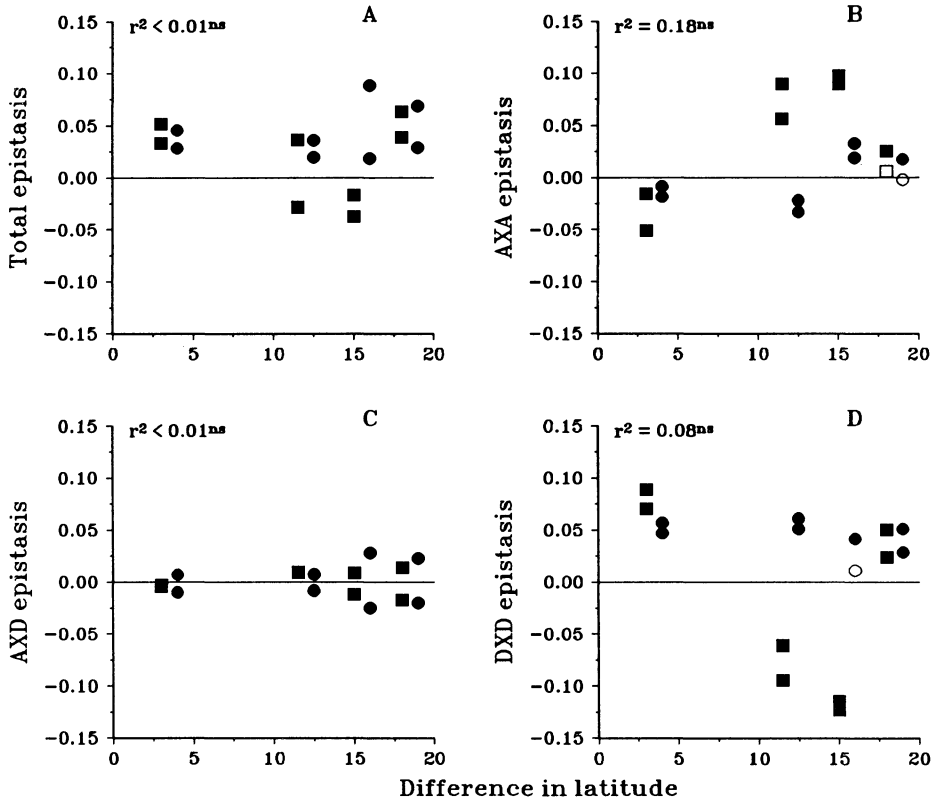


FIG. 3.—Digenic epistatic effects contributing to divergence in critical photoperiod as a function of difference in latitude for eight reciprocal crosses between southern and progressively more northern populations of *Wyeomyia smithii*: A, total epistasis; B, additive  $\times$  additive (A  $\times$  A) epistasis; C, additive  $\times$  dominance (A  $\times$  D) epistasis; D, dominance  $\times$  dominance (D  $\times$  D) epistasis. Solid symbols, significant ( $P < .05$ ) epistatic terms; open symbols, nonsignificant epistatic terms; solid circles, FL1 crosses; solid squares, FL2 crosses; NS, not significant at  $P > .05$ .

(fig. 3A) nor any of its components (fig. 3B–D) showed any detectable relationship to the geographical distance between crossed populations.

To examine the likely sources of epistasis, we performed multiple regression of heterosis on digenic epistasis for all crosses (Hayman 1960a; Hill 1982). Three measures of heterosis were used. Multiple regression of heterosis, measured as deviation of the  $F_1$  hybrid from the midparent, on the composite epistatic effects was poor ( $R^2 = 34\%$ ), and none of the effects made a significant contribution to heterosis (table 4). By contrast, heterosis measured as the difference between the  $F_2$  and the backcross means, a comparison in which all three lines are identical in heterozygosity, was highly correlated with one component of epistasis ( $R^2 > 98\%$ ). Additive  $\times$  additive, but not additive  $\times$  dominance or dominance  $\times$  dominance, effects made a highly significant contribution to this measure of heterosis (table 4). Heterosis measured as the differences between the  $F_1$  and  $F_2$  was

TABLE 4

RELATIONSHIPS OF COMPOSITE GENETIC EFFECTS TO THREE MEASURES OF HETEROISIS IN CRITICAL PHOTOPERIOD (log h), FOR THE 16 POPULATION CROSSES IN *WYEOMYIA SMITHII*

Variable	F <sub>1</sub> - MP	F <sub>2</sub> - mean BC	F <sub>2</sub> - F <sub>1</sub>
FL	-.004 ± .012 <sup>a</sup>	-.001 ± .002 <sup>a</sup>	.001 ± .006 <sup>a</sup>
A × A	.068 ± .346 <sup>a</sup>	-.250 ± .048***	-.532 ± .156***
A × D	.094 ± .346 <sup>a</sup>	.010 ± .048 <sup>a</sup>	-.027 ± .158 <sup>a</sup>
D × D	.112 ± .226 <sup>a</sup>	.001 ± .032 <sup>a</sup>	-.303 ± .102***
Total R <sup>2</sup>	.340 <sup>a</sup>	.989***	.821**

NOTE.—Entries are partial regression coefficients ( $\pm 2$  SE) from the regression of heterosis on additive  $\times$  additive (A  $\times$  A), additive  $\times$  dominance (A  $\times$  D), and dominance  $\times$  dominance (D  $\times$  D) epistasis. The designation FL indicates the effect of the particular southern parent used in the crosses (FL1 or FL2); MP, midparent; BC, backcross.

<sup>a</sup> Not significant at  $P > .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

also closely correlated with epistasis ( $R_2 > 82\%$ ). Both additive  $\times$  additive and dominance  $\times$  dominance, but not additive  $\times$  dominance, effects were highly significant (table 4). All significant regression coefficients of heterosis on epistatic effects across populations were negative (lines A  $\times$  A and D  $\times$  D in table 4). No significant effect of southern parent (line FL in table 4) on heterosis was evident, which indicates that the differentiation in critical photoperiod of northern populations from that of each southern population was qualitatively similar.

We do not report here estimates of the minimum number of effective factors contributing to divergence because they are unreliable when substantial nonadditive gene action is present (Lande 1981; Cockerham 1986; Zeng et al. 1990; see discussion in Hard et al. 1992).

#### DISCUSSION

The life cycles of temperate organisms generally include periods of active growth, development, and reproduction during favorable seasons, interspersed with periods of dormancy during unfavorable seasons. Among insects, diapause-mediated dormancy and migration not only provide escape in time and space but also affect rates of growth, development, and reproduction; synchronization with seasonal resources; and interactions with competitors, predators, and parasitoids (Tauber et al. 1986; Danks 1987). Thus, the ability of an organism to exploit favorable periods of weather, trophic resources, and enemy-free space may be conditional on a concordant phenology.

Many organisms use photoperiod as an indirect cue to anticipate future unfavorable conditions; insects known to use photoperiod to cue migration or diapause now number several hundred species (Masaki 1983). Where comparative data are available, the median or critical photoperiod for the initiation of diapause increases regularly with latitude and altitude of origin (Taylor and Spalding 1986). This regular pattern of critical photoperiods over ecoclimatic gradients suggests that they are a product of local optimizing selection and that locally adapted

means are relatively unperturbed by drift, mutation, and gene flow. Reasons for variation about the means are more elusive.

Estimates of the heritability of critical photoperiod are in the range of 0.3–0.7 (Tauber et al. 1986; Danks 1987), including previous estimates in *Wyeomia smithii* (Bradshaw and Holzapfel 1990; Scheiner and Istock 1991). In the present study, estimates among the six populations of *W. smithii* span this range, from 0.15 in western Florida to 0.79 in northern Massachusetts (fig. 1B). In *W. smithii*, both the mean (fig. 1A) and the additive genetic variance (fig. 1C) of critical photoperiod increase with geographical distance between northern and southern populations of *W. smithii*. The linear increase in mean critical photoperiod with latitude tracks closely the length of the favorable season along this cline (Bradshaw 1976; Bradshaw and Lounibos 1977). The south-to-north direction in evolution in *W. smithii* (Istock and Weisburg 1987; Bradshaw and Holzapfel 1990) means that the present pattern of critical photoperiod (fig. 1A) has resulted from directional selection for longer critical photoperiods. Yet, the present study confirms an earlier study (Bradshaw and Holzapfel 1990) in finding that directional selection on critical photoperiod during the northward expansion of *W. smithii* in North America has not reduced the genetic variation in this trait. Rather, additive genetic variance of critical photoperiod has increased substantially in progressively more derived populations, to a point where the additive genetic variance of the northernmost population exceeds the total genetic variance of either southern population.

The latitudinal increase in additive genetic variance is unlikely to be due to latitudinal changes in seasonality. Weather data taken over a 20-yr period at U.S. weather stations (U.S. Department of Commerce 1969–1988) over the range of *W. smithii* in the present study do show a consistent decrease in the date of the first frost (0°C) with increasing latitude (fig. 4A). The first frost does not, however, occur on the same date each year. Year-to-year variation in the end of the favorable season provides temporal variation in the optimal date to enter diapause. Such environmental variation might serve to maintain genetic variation for critical photoperiod (Haldane and Jayakar 1963; Bradshaw 1973; Gillespie 1973; Hedrick 1986; Sauer et al. 1986; but see Lande 1976; Slatkin and Lande 1976). Our calculations of the standard deviation in the date of first frost (fig. 4B) show a nonsignificant negative, not positive, correlation with latitude. Consequently, while variation in the end of season might contribute to the maintenance of genetic variation at any one locality, it cannot account for the increase in additive genetic variance with increasing latitude. Along the Gulf Coast, *W. smithii* completes five to seven generations per year but, at the latitude of the Ontario population, only one to two generations per year (Bradshaw 1983). Selection on critical photoperiod therefore occurs more frequently in the north than in the south. Because of decreasing density-dependent development with increasing latitude, development time is more deterministic in the north than in the south (Lounibos and Bradshaw 1975; Istock 1978; Bradshaw and Holzapfel 1986). With increasing latitude, photoperiod then becomes an increasingly accurate predictor of the end of the favorable season in terms of realized time remaining for development. Thus, if anything, both the frequency and the magnitude of optimizing selection on critical photope-

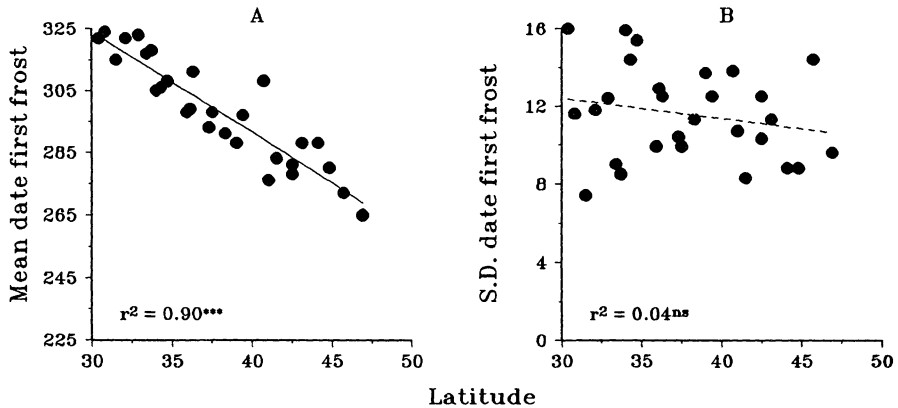


FIG. 4.—Mean (A) and standard deviation (B) of the date (day of calendar year; autumnal equinox, day 265) of first frost ( $0^{\circ}\text{C}$  or below) near pitcher-plant localities below 600 m at 28 sites east of the Appalachians in North America (FL, GA, SC, NC, VA, NJ, CT, MA, ME;  $30^{\circ}\text{N}$ – $47^{\circ}\text{N}$  latitude) and 13 localities west of the Appalachians (NY, MI, WI, MN;  $42^{\circ}\text{N}$ – $49^{\circ}\text{N}$  latitude). Data are based on an average of 18.2 observations per locality during the years 1969–1988; NS, not significant; \*\*\*  $P < .001$ .

riod should increase with latitude. The increase in additive genetic variance with latitude cannot then be explained by invoking mutation-selection balance (Lande 1976; Turelli 1984).

Epistatic genetic variance may also affect levels of additive genetic variance, especially in populations that experience repeated founder events (Robertson 1952; Goodnight 1988). The strict habitat requirements of *W. smithii* suggest that founder events may have been important during its northward evolution in North America. Because of this mosquito's tight host specificity, pitcher plants must have spread to new localities before establishment of mosquito populations. At the same time, pitcher-plant habitats are isolated, especially in the north, and *W. smithii* is a weak flyer "extremely prone to death by desiccation" (Istock and Weisburg 1987). Consequently, natural populations were probably founded by a few individuals, perhaps even occasionally by a single mated female, colonizing a resource-rich habitat. Indeed, on the basis of allozyme data from local and distant populations of *W. smithii*, Istock and Weisburg (1987) concluded that gene flow may be substantial within bogs but disrupted between even nearby bogs. Sequential establishment of populations along the latitudinal gradient is therefore likely to involve successive founder-flush episodes. While our results shed little light on the magnitude of epistasis within populations, they do indicate that epistatic variation in this trait is consistently high among divergent populations and does not vary with the geographical distance between them (fig. 3). Establishment of epistatic relationships therefore probably took place early in the process of genetic differentiation in *W. smithii* populations, at least from Florida to North Carolina. Subsequent differentiation of populations then resulted in progressive reorganization of epistatic interactions without increasing overall epistatic variation (fig. 3) and involved primarily additive  $\times$  additive and dominance  $\times$  domi-

nance interactions (table 4). Nonadditive genetic variation such as additive  $\times$  additive epistatic variance may also interact with drift to increase levels of additive genetic variance and subsequent selection responses (Robertson 1952; Griffing 1960; Cockerham 1984; Goodnight 1988). Indeed, populations that survive bottlenecks do not necessarily lose genetic variation (Sene and Carson 1977; Powell 1978; Craddock and Johnson 1979; Schwaegerle and Schaal 1979; Ringo et al. 1985; Carson and Wisotzkey 1989; Fleischer et al. 1991). However, the evidence for enhanced additive genetic variation as a result of a bottleneck (Lints and Bourgois 1982; Bryant et al. 1986a; López-Fanjul and Villaverde 1989) is much less substantial. The marked increase in additive genetic variance along the climatic gradient (fig 1C), together with the lack of accumulation of digenic epistatic effects along this gradient (fig. 3), suggests that epistatic variance may have been redistributed into additive variance during multiple founder events that have occurred during the dispersal and local adaptation of these populations. Northern, derived populations would have been founded more recently and, because of the cooler climate, would have undergone fewer generations per year than southern, ancestral populations. Consequently, northern populations have likely undergone fewer total generations since their establishment. We may therefore have sampled northern populations before the additive genetic variance had again become sequestered in dominance and epistatic relationships. In that case, the south-to-north distribution of *W. smithii* would represent a cline from ancestral populations at or near genetic equilibrium to progressively more disturbed states.

Regardless of the underlying causality, the present results establish the importance of nonadditive, epistatic effects in the genetic divergence of *W. smithii* over a broad ecoclimatic gradient (fig. 3). One of three crosses that could be tested for effects of higher-order epistasis and/or linkage shows evidence of these effects; digenic epistasis is sufficient to explain divergence in the other two (table 3). If this finding is general for quantitative traits affecting fitness, as suggested by Bryant et al. (1986a), Goodnight (1988), and Gimelfarb (1989), models of adaptive evolution that consider only additive genetic variation and covariation within populations (e.g., Lande 1980a, 1980b, 1982; Cheverud 1984; Rose 1985; Via and Lande 1985; Gillespie and Turelli 1989; Charlesworth 1990) may be of limited value in predicting how natural populations differentiate in life history.

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#### LITERATURE CITED

- Aitken, A. C. 1934. On least squares and linear combination of observations. *Proceedings of the Royal Society of Edinburgh* 55:42-48.

- Barker, J. S. F. 1974. The state of information concerning deviations from additivity of gene effects. *Proceedings of the 1st World Congress on Genetic Applications to Livestock Production* 1:373–383.
- . 1979. Inter-locus interactions: a review of experimental evidence. *Theoretical Population Biology* 16:323–346.
- Bradshaw, W. E. 1973. Homeostasis and polymorphism in vernal development of *Chaoborus americanus*. *Ecology* 54:1247–1259.
- . 1976. Geography of photoperiodic response in a diapausing mosquito. *Nature (London)* 262:384–386.
- . 1983. Interaction between the mosquito *Wyeomyia smithii*, the midge, *Metricnemus knabi*, and their carnivorous host *Sarracenia purpurea*. Pages 161–189 in J. H. Frank and L. P. Lounibos, eds. *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, N.J.
- Bradshaw, W. E., and C. M. Holzapfel. 1986. Geography of density-dependent selection in pitcher-plant mosquitoes. Pages 48–65 in F. Taylor and R. Karban, eds. *The evolution of insect life cycles*. Springer, New York.
- . 1989. Life-historical consequences of density-dependent selection in the pitcher-plant mosquito, *Wyeomyia smithii*. *American Naturalist* 133:869–887.
- . 1990. Evolution of phenology and demography in the pitcher-plant mosquito, *Wyeomyia smithii*. Pages 47–67 in F. Gilbert, ed. *Insect life cycles: genetics, evolution, and coordination*. Springer, London.
- Bradshaw, W. E., and L. P. Lounibos. 1977. Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution* 31:546–567.
- Bryant, E. H., S. A. McCommas, and L. M. Combs. 1986a. The effect of an experimental bottleneck upon quantitative genetic variation in the housefly. *Genetics* 114:1191–1211.
- Bryant, E. H., L. M. Combs, and S. A. McCommas. 1986b. Morphometric differentiation among experimental lines of the housefly in relation to a bottleneck. *Genetics* 114:1213–1223.
- Carson, H. L., and R. Lande. 1984. Inheritance of a secondary sexual character in *Drosophila silvestris*. *Proceedings of the National Academy of Sciences of the USA* 81:6904–6907.
- Carson, H. L., and R. G. Wisotzkey. 1989. Increase in genetic variance following a population bottleneck. *American Naturalist* 134:668–673.
- Cavalli, L. L. 1952. An analysis of linkage in quantitative inheritance. Pages 135–144 in E. C. R. Reeve and C. H. Waddington, eds. *Quantitative inheritance*. Her Majesty's Stationery Office, London.
- Charlesworth, B. 1990. Optimization models, quantitative genetics, and mutation. *Evolution* 44:520–538.
- Cheverud, J. 1984. Quantitative genetics and developmental constraints on evolution by selection. *Journal of Theoretical Biology* 110:155–171.
- Cockerham, C. C. 1980. Random and fixed effects in plant genetics. *Theoretical and Applied Genetics* 56:119–131.
- . 1984. Additive by additive variance with inbreeding and linkage. *Genetics* 108:487–500.
- . 1986. Modifications in estimating the number of genes for a quantitative character. *Genetics* 114:659–664.
- Cohan, F. M., A. A. Hoffmann, and T. W. Gayley. 1989. A test of the role of epistasis in divergence under uniform selection. *Evolution* 43:766–774.
- Craddock, E. M., and N. E. Johnson. 1979. Genetic variation in Hawaiian *Drosophila*. V. Chromosomal and allozyme diversity in *Drosophila silvestris* and its homosequential species. *Evolution* 33:137–155.
- Danks, H. V. 1987. Insect dormancy: an ecological perspective. *Biological Survey of Canada Monograph Series no. 1*.
- Falconer, D. S. 1981. *Introduction to quantitative genetics*. 2d ed. Longman, New York.
- Fisher, R. A. 1958. *The genetical theory of natural selection*. 2d ed. Dover, New York.
- Fleischer, R. C., S. Conant, and M. P. Morin. 1991. Genetic variation in native and translocated populations of the Laysan finch (*Telespiza cantans*). *Heredity* 66:125–130.
- Gillespie, J. 1973. Polymorphism in random environments. *Theoretical Population Biology* 4:193–195.



- Gillespie, J. H., and M. Turelli. 1989. Genotype-environment interactions and the maintenance of polygenic variation. *Genetics* 121:124–138.
- Gimelfarb, A. 1985. Is offspring-midparent regression affected by assortative mating of parents? *Genetical Research* 47:71–75.
- . 1989. Genotypic variation for a quantitative character maintained under stabilizing selection without mutations: epistasis. *Genetics* 123:217–227.
- Goodnight, C. 1988. Epistasis and the effect of founder events on the additive genetic variance. *Evolution* 42:441–454.
- Griffing, B. 1960. Theoretical consequences of truncation selection based on the individual phenotype. *Australian Journal of Biological Sciences* 13:307–343.
- Haitovsky, Y. 1973. Regression estimation from grouped observations. Griffin's Statistical Monograph no. 33. Hafner, New York.
- Haldane, J. B. S., and S. D. Jayakar. 1963. Polymorphism due to selection of varying direction. *Journal of Genetics* 58:237–242.
- Hannan, M. T., and L. Burstein. 1974. Estimation from grouped observations. *American Sociological Review* 39:374–392.
- Hard, J. J., W. E. Bradshaw, and C. M. Holzapfel. 1992. Epistasis and the genetic divergence of photoperiodism between populations of the pitcher-plant mosquito, *Wyeomyia smithii*. *Genetics* 131:389–396.
- Hayman, B. I. 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12:371–390.
- . 1960a. The separation of epistatic from additive and dominance variation in generation means. II. *Genetica* 31:133–146.
- . 1960b. Maximum likelihood estimation of genetic components of variation. *Biometrics* 16:369–381.
- Hedrick, P. W. 1986. Genetic polymorphism in heterogeneous environments: a decade later. *Annual Review of Ecology and Systematics* 17:535–566.
- Hedrick, P., S. Jain, and L. Holden. 1978. Multilocus systems in evolution. *Evolutionary Biology* 11:101–182.
- Hill, W. G. 1982. Dominance and epistasis as components of heterosis. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 99:161–168.
- Istock, C. A. 1978. Fitness variation in a natural population. Pages 171–190 in H. Dingle, ed. *Evolution of insect migration and diapause*. Springer, New York.
- Istock, C. A., and W. G. Weisburg. 1987. Strong habitat selection and the development of population structure in a mosquito. *Evolutionary Ecology* 1:348–362.
- Kearsey, M. J., and K.-I. Kojima. 1967. The genetic architecture of body weight and egg hatchability in *Drosophila melanogaster*. *Genetics* 56:23–37.
- Lande, R. 1976. The maintenance of genetic variability by mutation in a polygenic character with linked loci. *Genetical Research* 26:221–235.
- . 1980a. Genetic variation and phenotypic evolution during allopatric speciation. *American Naturalist* 116:463–479.
- . 1980b. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94:203–215.
- . 1981. The minimum number of genes contributing to quantitative variation between and within populations. *Genetics* 99:541–553.
- . 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607–615.
- Lints, F. A., and M. Bourgois. 1982. A test of the genetic revolution hypothesis of speciation. Pages 423–436 in S. Lakovaara, ed. *Advances in genetics, development and evolution of Drosophila*. Plenum, New York.
- López-Fanjul, C., and A. Villaverde. 1989. Inbreeding increases genetic variance for viability in *Drosophila melanogaster*. *Evolution* 43:1800–1804.
- Lounibos, L. P., and W. E. Bradshaw. 1975. A second diapause in *Wyeomyia smithii*: seasonal incidence and maintenance by photoperiod. *Canadian Journal of Zoology* 53:215–221.
- Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution* 45:622–629.

- Masaki, S. 1983. Introduction. Pages 1–5 in V. K. Brown and I. Hodek, eds. *Diapause and life cycle strategies in insects*. Junk, The Hague.
- Mather, K., and J. L. Jinks. 1982. *Biometrical genetics: the study of continuous variation*. 3d ed. Chapman & Hall, New York.
- Powell, J. R. 1978. The founder-flush speciation theory: an experimental approach. *Evolution* 32:465–474.
- Prais, S. J., and J. Aitchison. 1954. The grouping of observations in regression analysis. *Revue de l'Institut International de Statistique* 22:1–22.
- Ringo, J., D. Wood, R. Rockwell, and H. Douse. 1985. An experiment testing two hypotheses of speciation. *American Naturalist* 126:642–661.
- Robertson, A. 1952. The effect of inbreeding on the variation due to recessive genes. *Genetics* 37:189–207.
- Rose, M. R. 1985. Life history evolution with antagonistic pleiotropy and overlapping generations. *Theoretical Population Biology* 28:342–358.
- Sauer, K. P., H. Spieth, and C. Grüner. 1986. Adaptive significance of genetic variability of photoperiodism in Mecoptera and Lepidoptera. Pages 153–172 in F. Taylor and R. Karban, eds. *The evolution of insect life cycles*. Springer, New York.
- Scheiner, S. M., and C. A. Istock. 1991. Correlational selection of life history traits in the pitcher-plant mosquito. *Genetica* 84:123–128.
- Schwaegerle, K. E., and B. A. Schaal. 1979. Genetic variability and founder effect in the pitcher plant, *Sarracenia purpurea* L. *Evolution* 33:1210–1218.
- Sene, F. M., and H. L. Carson. 1977. Genetic variation in Hawaiian *Drosophila*. IV. Allozymic similarity between *D. silvestris* and *D. heteroneura* from the island of Hawaii. *Genetics* 86:187–198.
- Slatkin, M., and R. Lande. 1976. Niche width in a fluctuating environment—density independent model. *American Naturalist* 110:31–55.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal adaptations of insects*. Oxford University Press, New York.
- Taylor, F., and J. Spalding. 1986. Geographic patterns in the photoperiodic induction of hibernial diapause. Pages 66–85 in F. Taylor and R. Karban, eds. *The evolution of insect life cycles*. Springer, New York.
- Turelli, M. 1984. Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle. *Theoretical Population Biology* 25:138–193.
- U.S. Department of Commerce. 1969–1988. *Climatological data*. National Oceanic and Atmospheric Administration, Environmental Data Service, Asheville, N.C.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–523.
- Wade, M. J., and D. E. McCauley. 1984. Group selection: the interaction of local deme size and migration in the differentiation of small populations. *Evolution* 38:1047–1058.
- Wright, S. 1968. *Evolution and the genetics of populations*. Vol. 1. Genetic and biometric foundations. University of Chicago Press, Chicago.
- . 1977. *Evolution and the genetics of populations*. Vol. 3. Experimental results and evolutionary deductions. University of Chicago Press, Chicago.
- Zeng, Z.-B., D. Houle, and C. C. Cockerham. 1990. How informative is Wright's estimator of the number of genes affecting a quantitative character? *Genetics* 126:235–247.

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