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William E. Bradshaw

Department of Biology, University of Oregon, Eugene, OR 97403, USA

"The combined essences of heaven and earth became the yin and yang; the concentrated essences of the yin and the yang became the four seasons, and the scattered essences of the four seasons became the myriad creatures of the world." *Huai-nan Tzu* 3:1a, ca. 120 BC

The great fluctuations of light, temperature, and moisture in the biosphere result from the periodic rotations of the sun, the earth, and the moon. The rotation of the earth about the sun gives rise to the four seasons and the rotation of the earth about its own axis gives rise to the daily cycles. At any point on the earth, there are seasons that are favorable for growth, development, and reproduction, and seasons that are unfavorable for these processes. Fitness in a seasonal environment then consists of 3 major components:

1. maximizing the opportunity for growth, development, and reproduction during the favorable season;
2. minimizing the loss of growth, development, and reproduction during the unfavorable season;
3. optimizing the conversion of life-styles between the seasons.

The Favorable Season (陽)

"Of the four seasons, none lasts forever; of the days, some are long and some are short." *Sun Tzu* 6:31

During the favorable season, the most inclusive measure of fitness is usually taken to be the Malthusian parameter, r , found by iterative solution of the Euler equation,

$$\sum l_x m_x e^{-rx} = 1$$

where l_x and m_x are the per-capita rates of survivorship to and reproduction at age x . r may be approximated by Laughlin's capacity for increase, r_c , where

$$r_c = \ln R_0 / \tau$$

R_0 = cohort replacement rate = $\sum l_x m_x \approx$
(survivorship)(fecundity)

τ = cohort generation time = $\sum x l_x m_x / \sum l_x m_x$
= time from oviposition of parent to
production of mean offspring egg

Because of their direct contribution to r_c or r , age-specific survivorship and reproduction are often termed "fitness traits." Fitness traits are assumed to be undergoing continuous directional selection. Because of this selection, they should exhibit low or zero heritability (additive genetic variance + phenotypic variance). Contrary to this

expectation, fitness traits exhibit significant and sometimes substantial heritabilities. A prominent explanation for the persistence of finite heritability for fitness traits involves the concept of genetic tradeoffs. Genetic tradeoffs arise from loci with pleiotropic effects, that is, one gene affecting several traits. If a pleiotropic allele has a beneficial effect on fitness through two or more traits, that allele should become fixed in a population; conversely, if a pleiotropic allele has a deleterious effect on fitness through two or more traits, that allele should go extinct in a population. In either case, fixation or extinction, the locus in question is monomorphic and makes no contribution to additive genetic variance in the population. By contrast, if a pleiotropic allele has a beneficial effect on one trait and, at the same time, a deleterious effect on another trait, selection cannot simultaneously optimize both traits. As a consequence of these "antagonistic" pleiotropic effects, the frequency of the allele should persist at some intermediate level in the population and contribute to additive genetic variance in both traits. At the genetic level, pleiotropic effects on fitness traits are revealed as genetic correlations among them; at the phenotypic level, pleiotropic effects on fitness traits are revealed as tradeoffs among them - improvement of one trait through selection leads to a compensating decline in the other.

There is now a rapidly expanding literature on "antagonistic pleiotropy," genetic correlations, and genetic tradeoffs among traits contributing to r , especially among traits affecting reproduction¹. What these studies usually fail to take into account is that no season lasts forever.

The Unfavorable Season (陰)

"I know the value of nonaction." *Lao Tzu* 43

The unfavorable season is generally perceived as an exigency against which an insect must make an active (有為) response, usually through diapause or migration, "escape in time or space." Conceptually, cold would be dealt with through cold-hardiness, drought through tolerance to desiccation, low food through sequestered lipid and protein, and so on. Yet, for a surprising number of insects, the aestivating or hibernating forms do not express obvious countermeasures to the unfavorable conditions. In the pitcher-plant mosquito, *W. smithii*, diapause does not

confer increased cold-hardiness in either the freezing-point depression or in the ability to supercool². Likewise, the pitcher-plant midge, *Metriocnemus knabi*, enters diapause only in the fourth instar but overwinters successfully in all instars (Bradshaw and Holzapfel, unpublished). In the southern part of their range, both pitcher-plant insects experience mild winters. In the northern part of their range, winters are severe but pitcher plants lie between a blanket of insulating snow and a reservoir of heat in the underlying bog. Rather than conferring resistance to winter, diapause permits non-development in a relatively safe locality, escape in time and space. The overwintering larvae might be viewed more appropriately as non-adults avoiding the non-favorable season through non-action (無為).

Return of the Favorable Season

"Reversal is the movement of the Tao." *Lao Tzu* 40

Just as the favorable season gives way to the unfavorable season, so too does the favorable season inexorably return. Synchrony in vernal development may permit temporal overlap of the sexes, seasonally abundant resources, and saturation of predators. Elaborate photoperiodic responses may achieve synchrony in semivoltine crickets and dragonflies; vernal synchrony in faster-developing insects may be achieved through more passive mechanisms. The planktonic midge, *Chaoborus americanus*, overwinters in a fourth instar diapause that is initiated, maintained, and terminated by photoperiod. Resumption of development in the spring involves 3 stages: (1) Termination of diapause itself, (2) completion of post-diapause morphogenesis leading to the larval-pupal molt, and (3) completion of adult development leading to adult ecdysis. The progression of this sequence takes place during the spring when temperature, although variable, continues to rise over the period of several weeks. Variation in response to photoperiodic and trophic cues will lead to variation in the start of diapause termination. Some individuals will resume development earlier than others. Later developing individuals will, however, encounter warmer temperatures at each specific state in the sequence. Thus, later developing individuals will develop faster than and overtake (but can never pass) the earlier developing individuals (Fig. 1). Vernal synchrony in *C. americanus* is achieved through the action of rising vernal temperatures and non-action (無為) by the overwintering insects.

Reversal is the progression of the seasons. The migrating or diapausing generation must still reproduce. Even the most dormant individual must hold within itself the full phenotypic repertoire to exploit the coming favorable season. Non-action must return to action. Too often, diapause and migration are seen as the singular adaptation to winter; survivorship becomes the paramount life-history trait in the mind of the investigator; the

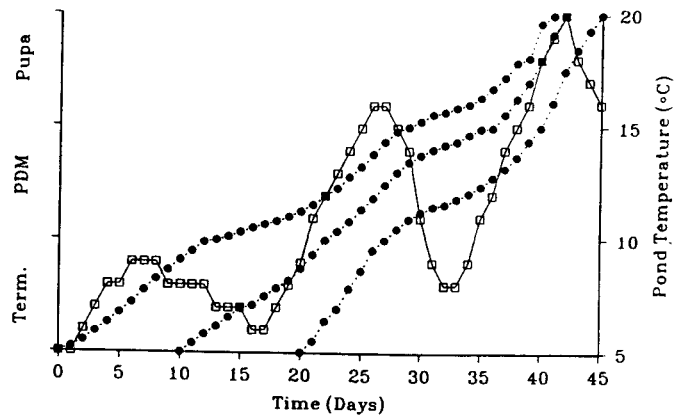


Figure 1. Development of *Chaoborus americanus* in a shallow vernal pond with fluctuating but increasing temperature (Michigan, USA)¹². The left axis plots percentage completion of the termination of fourth instar diapause (Term.), percentage completion of post-diapause morphogenesis (PDM) leading to pupation, and percentage completion of the pupal stage (Pupa) leading to adult ecdysis. Different larvae commencing development on days 0, 10, and 20 emerge as adults on days 41, 42, and 45 due to the autosynchronizing effects of rising temperature.

necessity to complete the life cycle is overlooked. Without eventual reproduction, there is no survivorship through the unfavorable season. Analogously to capacity for increase during the favorable season (r_c), there is capacity for increase during the generation that passes through the unfavorable season,

$$r_u = \ln R_u / \tau_u$$

R_u = (probability of surviving diapause)(expected per-capita fecundity of the survivors)

τ_u = time from the resumption of the favorable season to the production of the mean propagule.

Thus, insects encountering an unfavorable season must not only survive, they must also reproduce and do so in a timely manner. Maximum survivorship and reproduction and minimum net generation time are no less important in diapausing than in continuously developing generations. Very few investigators have considered the cost of diapause in terms of post-diapause reproductive success but this residual reproductive value is an integral component of fitness in the dormant or migrating generation³. Each generation achieves its own rate of increase and annual fitness is the mean r of the constituent generations. Minimizing the decline of r during the unfavorable season may then make as much or more of a contribution to fitness as maximizing the gain in r during the favorable season. Nutritional reserves, sequestered during the late summer and autumn contribute both to survival during the winter and to individual fitness on the return of spring, the reversal of winter.

Harmony (真和) and non-harmony (無和)

"It is in leaving that we return." *Chuang Tzu* 33

Superficially, it is through the cycling of development (有為) and diapause (無為) that harmony is achieved with a seasonal environment. This harmony can not, however, persist without non-harmony. Antagonistic pleiotropy may be responsible for the maintenance of significant and even substantial additive genetic variance for fitness traits in populations. When genetic correlations or tradeoffs are not observed between two fitness traits, it is usually concluded that the crucial genetic correlation or tradeoff must occur "elsewhere in the life cycle." A non-tradeoff between egg size and number of eggs in a clutch may mean that larger individuals are able to produce both more and larger eggs but may require longer pre-adult development to do so. The tradeoff exists but it is between adult size and development time, not between egg size and egg number. Tradeoffs may occur anywhere in complex life cycles and may include groups of traits. Thus, non-tradeoffs between any two specific traits may be due to a tradeoff at a more inclusive level of life-cycle organization.

What is the most inclusive level of life-cycle integration? I would argue that, in a seasonal environment, the most complete level of integration requires at least one entire annual cycle. Tradeoffs are to be expected among the 3 major components of the life cycle listed on the first page. Thus, maximization of r during the favorable season, maximization of r during the unfavorable season, and optimization of the critical photoperiod should be the most inclusive components of fitness in a seasonal environment (Fig. 2).

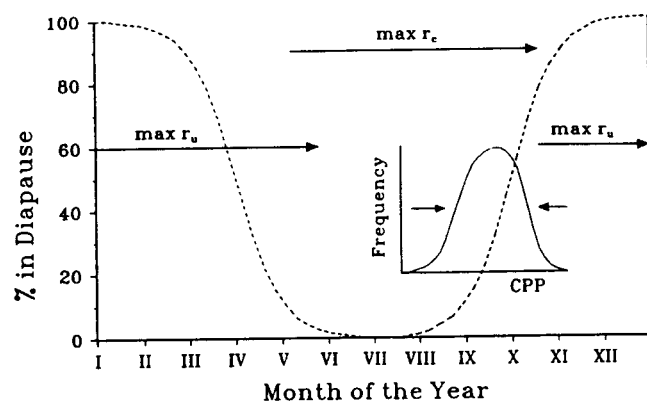


Figure 2. In a seasonal environment, fitness involves the maximization of r_c during the favorable season, the maximization of r_u during the unfavorable season, and the optimization of the critical photoperiod. At the highest level of life-cycle integration, these three major components of fitness may trade off with one another and, therefore, mutually constrain each other's evolution.

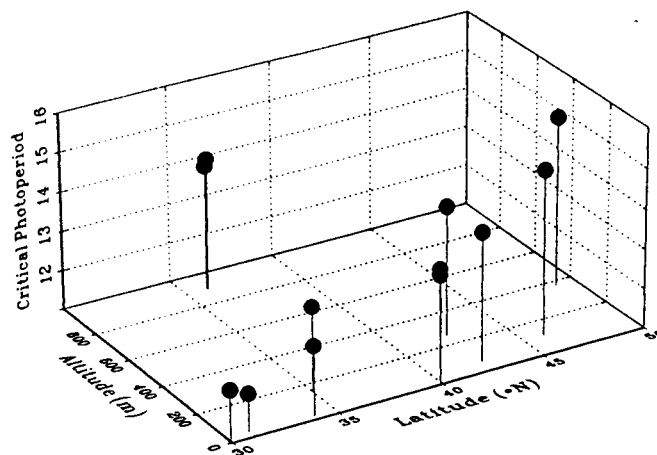


Figure 3. Effect of geography on critical photoperiod in 12 populations of *Wyeomyia smithii* in North America⁴. Critical photoperiod tracks latitude and altitude very closely ($R^2 = 0.96$; $P < 0.001$).

The pitcher-plant mosquito completes its preadult development within the water-filled leaves of the purple pitcher plant, *Sarracenia purpurea*. This single species of mosquito occupies this consistent, circumscribed habitat over a range of 25° latitude and 1,500 m altitude. Geographic distribution and morphological, physiological, and behavioral traits all indicate that *W. smithii* has evolved from south to north⁴. Because of the unusual consistency of their habitat, variation in life history over the range of *W. smithii* should reveal the direct effects of geography on their evolution. In the extreme southern end of their range, development and pupation success are strongly affected by larval density. Not even diapause provides an escape in time or space from density-dependent constraints. These constraints abate with increasing latitude or altitude and in some high elevations or far northern populations, there is no evidence for density-dependent development at any time of year⁵. The evolutionary pathway of *W. smithii* has therefore encompassed two major gradients: the ecological gradient of decreasing density-dependent development and the climatic gradient of an advancing autumn and receding spring. Over this ecoclimatic gradient, critical photoperiod tracks latitude and altitude tightly (Fig. 3) while there is no geographic pattern in r_c or density-tolerance (Fig. 4). Thus, critical photoperiod has adapted to the climatic gradient while r_c has not responded to the ecological gradient of density-dependent selection. Still, individual populations vary in r_c and in the tolerance of r_c to increasing density^{4,6}. This between-population variation in r_c and in density-tolerance means that both traits can and have evolved. The evolution in r_c has been independent of both the ecological gradient in density-dependent development and the climatic gradient in seasonality and, consequently of critical photoperiod.

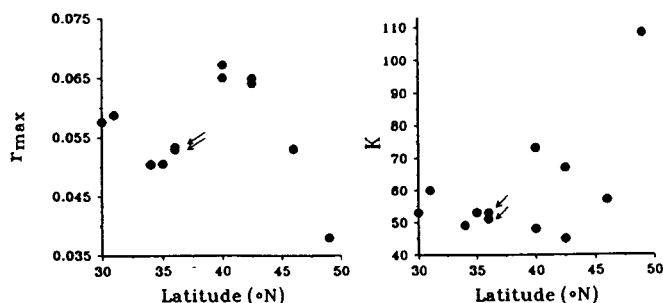


Figure 4. Effect of geography on r_{\max} and K in the same populations of *W. smithii* shown in Figure 3. r_{\max} is the maximum cohort capacity for increase achieved at any density; K is the density (interpolated) at which capacity for increase equals zero. The arrows indicate the two alpine populations. Both r_{\max} ($R^2 = 0.16$; $P > 0.05$) and K ($R^2 = 0.32$; $P > 0.05$) track latitude and altitude very poorly⁴.

Selection on rapid development in *W. smithii* elicits a correlated response in both r_c (Bradshaw and Holzapfel, unpublished) and critical photoperiod⁷. Thus, the independent evolution of critical photoperiod and r_c has taken place despite, and not because of, their underlying genetic correlation. The explanation for the paradoxical independent evolution of genetically correlated traits may lie in the evolutionary dynamics of the underlying genetic architecture during the northward invasion of North America by *W. smithii*.

Genetic variation affecting life-history traits includes additive, dominance, and epistatic effects. Additive effects of genes are independent of genetic effects of other alleles or of other loci. Dominance effects reflect interaction among alleles within the same locus and epistatic effects reflect interaction among loci. Adaptation in the broad sense involves not only optimization of the phenotype with respect to the local habitat or "local adaptation" but also the optimization of gene-gene interactions in the internal genetic environment. This "genetic coadaptation" results in "coadapted gene complexes" whose cohesiveness is fundamental to their harmonious interaction⁸⁻⁹. Additive, dominance, and epistatic effects have been involved in the adaptive evolution of photoperiodic response in *W. smithii*.

Wyeomyia smithii is dependent upon pitcher plants for its survival. This dependence means that, following the receding of the last glacial ice sheet from northern North America 10-12,000 years ago, the plants must have become established before *W. smithii* could invade a habitat. At the same time, *W. smithii* is a weak-flying mosquito, extremely prone to death by desiccation. The sequential colonization of habitats thus probably represented the immigration of a few or even a single individual. It is under exactly these circumstances that we can expect disruption of genomes and genetic drift to take place¹⁰. Independent evolution of isolated populations of *W. smithii* should be reflected in the evolution of new genetic

interactions within and between loci; these interactions should become apparent when distant north-south populations are hybridized. Figure 5 shows the mean and variance of critical photoperiod of a southern (30° N latitude) and a northern (49° N latitude) population of *W. smithii* along with their F_1 and F_2 hybrids. High fitness of the critical photoperiod is represented by higher precision and, consequently, by a lower variance about the mean phenotype. In Figure 5, if evolution of critical photoperiod from south to north had involved only additive genetic effects, then mean of the F_1 and F_2 generations should both be 0.00 and their variance should lie on the zero intercept of the dashed line connecting the two parent values. The lower than expected variance in the F_1 indicates a significant increase in precision (hybrid vigor or heterosis) and, consequently, a contribution of dominance to evolutionary divergence of critical photoperiod. If evolution of critical photoperiod from south to north had involved only additive and dominance genetic effects, then the F_2 variance should lie half-way between the F_1 and the dashed line¹¹. The higher than expected variance in the F_2 indicates a significant loss in precision (outbreeding depression) and, consequently, a contribution of gene-gene interaction (epistasis) to evolutionary divergence of critical photoperiod. Evolution of critical photoperiod over the south to north migration of *W. smithii* has therefore involved the rearrangement of additive, dominance, and epistatic effects.

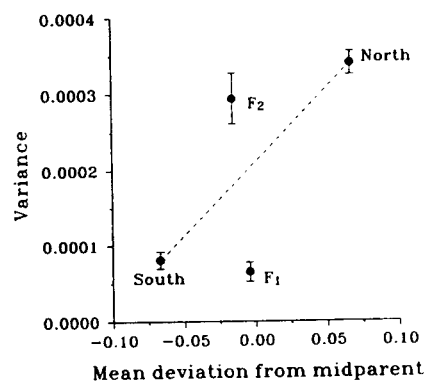


Figure 5. Mean and variance in critical photoperiod of *W. smithii* from a southern (30° N Latitude) and a northern (49° N Latitude) population and in their F_1 and F_2 hybrids¹³. The error bars show ± 2 SE; the error bars of the means are all contained within the space of the solid circles.

At temperate latitudes in the central and eastern portion of continental land masses (Asia as well as North America), mid-summer temperatures remain quite similar while winter temperatures decline more dramatically with increasing latitude (Fig. 6). Thus, the thermal environment during the favorable season is similar over a wide range of latitudes and the main climatic variable is the decreasing

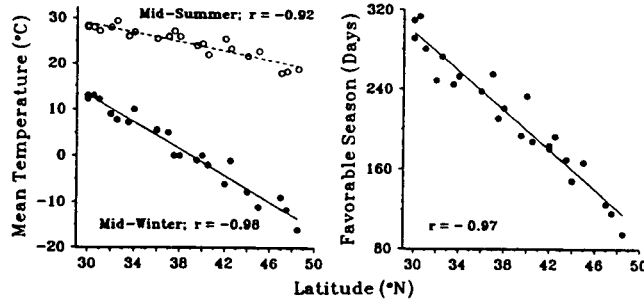


Figure 6. Climatic patterns in central and eastern North America¹⁴. The plots incorporate 11 localities on the eastern continental slope (31-48° N) and 11 localities in the north-central plains (40-49° N) where *W. smithii*'s host plant, *S. purpurea* is found. Mid-summer and mid-winter temperatures are the mean temperature of the warmest (July) and coldest (January) month of the year, respectively. The favorable season is measured as the mean number of days between the last frost (0° C) in the spring and the first frost in the fall.

duration of that favorable season with increasing latitude. Consequently, the greatest evolutionary divergence among insect populations over temperate latitudes should be those traits involved in the regulation of seasonal development rather than traits involved in growth, development, and reproduction during the favorable season. Indeed, that pattern is exactly the one observed in *W. smithii*. Critical photoperiod tracks geography very closely (Fig. 3) while r_c varies, but independently of geography (Fig. 4). Similarity of r_c over a wide geographic range then reflects (1) the similarity of the favorable season over this range and (2) the success of latitude- and altitude-specific photoperiodic response to program growth, development, and reproduction in harmony with the favorable season.

Despite the relative similarity of r_c among populations, there are still significant differences among them. Capacity for increase is composed of two components, R_0 and τ , which are, in turn, composed of several subcomponents

$$R_0 = (\% \text{ survivorship to adult})(\% \text{ females among eclosing adults})(\text{eggs per eclosed female})$$

$$\tau = (\text{days from oviposition to median eclosion of parents}) + (\text{days from median eclosion of parents to production of median offspring egg}).$$

Although r_c , R_0 , and τ all vary among populations of *W. smithii*, there is no significant among-population covariation in R_0 and τ ; nor, is there any significant among-population covariation between any two subcomponents of r_c (Fig. 7). Thus, r_c varies among populations but this variation represents a population-specific, independently evolved assembly of its components and sub-components.

The pattern of r_c , its components, and its subcomponents over the range of *W. smithii* is consistent with the genetic architecture underlying photoperiodic response and leads to the following scenario. At each locality in the northward advance of *W. smithii*, a few founding individuals encountered an unoccupied, resource-rich habitat. Following the initial colonization, a restricted founder genome and genetic drift resulted first in the break up of genetic correlations and coadapted gene complexes and second in the establishment of a uniquely new genetic architecture. This genetic architecture represented locality-specific genetic tradeoffs and locality-specific interactions within and between loci. While in genetic disequilibrium, selection could operate on r_c independently of critical photoperiod, thereby permitting their independent evolution and the independent evolution of r_c , its components, and its subcomponents among disparate populations of *W. smithii*.

The evolutionary history of many insects involves episodes of local extinction and recolonization or the invasion of new habitats. Well-adapted populations may be seen as having a harmonious phenotype and an underlying harmonious genetic architecture. Still, there persists non-harmony in the form of mutation, genetic tradeoffs, and alleles suppressed through dominance or epistatic interactions. It is from the genetic variation contained within the genetic tradeoffs and suppressed alleles that colonizing populations are able to construct new and unique genetic architectures in relation to both the external habitat and internal genetic environment. At any time and place, selection may favor the harmonious relationship between the organism and its habitat and among the genetic contributors to that relationship. Within this harmony, there is non-harmony and it is from the non-harmony that evolutionary flexibility arises.

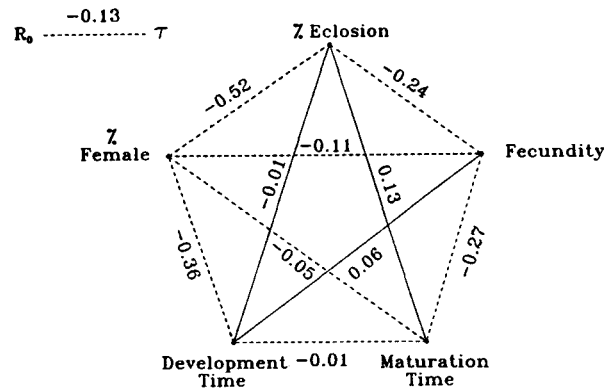


Figure 7. Interpopulation correlation of the components (R_0 , τ) and 5 subcomponents of r_c among the populations shown in Figure 4. The numbers show pairwise correlation coefficients. Dashed lines represent negative correlations; solid lines represent positive correlations. None of the correlations is significant. Thus, r_c , R_0 , and τ that do vary among populations, are constructed of the components and subcomponents independently at each locality⁴.

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REFERENCES

1. Roff, D. A., 1992. The Evolution of Life Histories. Chapman & Hall, NY.
2. Evans, K. W., and R. A. Brust, 1972. Induction and termination of diapause in *Wyeomyia smithii* (Diptera: Culicidae), and larval survival studies at low and subzero temperatures. Can. Entomol. 104:1937-1950.
3. Denlinger, D. L., 1981. Basis for a skewed sex ratio in diapause-destined flesh flies. Evolution 35:1247-1248.
4. Bradshaw, W. E., and C. M. Holzapfel, 1990. Evolution of phenology and demography in the pitcher-plant mosquito, *Wyeomyia smithii*. In: Insect Life Cycles: Genetics, Evolution, and Coordination (Ed. F. Gilbert), pp.47-67. Springer-Verlag, London.
5. Bradshaw, W. E., and C. M. Holzapfel, 1986. Geography of density-dependent selection in pitcher-plant mosquitoes. In: The Evolution of Insect Life Cycles (Eds. F. Taylor and R. Karban), pp. 48-65. Springer-Verlag, New York.
6. Bradshaw, W. E., and C. M. Holzapfel, 1989. Life-historical consequences of density-dependent selection in the pitcher-plant mosquito, *Wyeomyia smithii*. Am. Nat. 133:869-887.
7. Hard, J. J., W. E. Bradshaw, and C. M. Holzapfel, 1994. Genetic coordination of demography and phenology in the pitcher-plant mosquito, *Wyeomyia smithii*. J. Evol. Biol. (in press).
8. Mayr, E., 1963. Animal Species and Evolution. Harvard University Press, Cambridge.
9. Dobzhansky, Th., 1970. Genetics of the Evolutionary Process. Columbia University Press, New York.
10. Carson, H. L., and A. R. Templeton, 1984. Genetic revolutions in relation to speciation phenomena: the founding of new populations. Ann. Rev. Ecol. Syst. 15:97-131.
11. Lynch, M., 1991. The genetic interpretation of inbreeding depression and outbreeding depression. Evolution 45:622-629.
12. Bradshaw, W. E., 1973. Homeostasis and polymorphism in vernal development of *Chaoborus americanus*. Ecology 54:1247-1259.
13. 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.
14. NOAA, 1968. Climatic Atlas of the United States. Environmental Sciences Service Administration, Environmental Data Service. U. S. Department of Commerce, Washington, DC

季節環境の中での進化

鹿田正雄