

SPECIALISTS AND GENERALISTS IN CHANGING ENVIRONMENTS. I. FITNESS LANDSCAPES OF THERMAL SENSITIVITY

GEORGE W. GILCHRIST*

Department of Zoology, Box 351800, University of Washington, Seattle, Washington 98195-1800

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Abstract.—Animals and plants often exhibit narrow ranges of thermal preference in variable environments; fitness-enhancing activities such as reproduction and growth tend to be concentrated during times in which body temperature lies within that narrow range. The relation between fitness-associated performance and temperature is modeled by a performance curve defined by two traits: performance breadth (T_{br}), a measure of thermal specialization, and the critical maximum temperature for performance (T_{max}). Optimality models are used to define the fitness landscape for these two traits under several different patterns of within- and among-generation variation in temperature. In constant environments and environments in which there is significant within-generation variation, specialists with narrow preference ranges are the favored phenotype. In environments in which there is considerable among-generation but little within-generation variation, generalists with broad preference ranges are favored. Specialists in a constant environment have a mean fitness an order of magnitude higher than any phenotype in more variable environments, demonstrating that homeostatic mechanisms can confer a large fitness advantage. In contrast to previous models of environmental tolerance, these performance models suggest that increasing temporal environmental variation can favor the evolution of thermal specialization.

Animals and plants often concentrate fitness-enhancing activities, such as growth, mating, foraging, and reproduction, over a narrow, "preferred" range of body or environmental temperatures (Andrewartha and Birch 1954; Magnuson et al. 1979). In seasonal climates, daily and annual temperature cycles may limit the preferred conditions to a few hours a day during a few weeks of the year. Endothermy and behavioral thermoregulation provide solutions for dealing with a variable environment by reallocating time and energy to regulate body temperatures within the narrow preferred range. The maintenance of relatively constant body temperature allows the optimization of critical catalytic and metabolic processes (Hochachka and Somero 1984), enhancing both the efficiency of and the time available for activities that enhance fitness (Hawkins et al. 1993). These benefits of thermoregulation are presumably great enough to offset the considerable costs of homeostasis; yet for many species, thermoregulatory mechanisms are unavailable or ineffective. Small body size, an aquatic habitat, limited motility, and shaded environments are among the factors that may limit the capacity to regulate body temperature (Willmer and Unwin 1981; Unwin and Corbet 1984). Such species provide an excellent opportunity to estimate the costs and benefits of

* E-mail: gilchgw@zoology.washington.edu.

different preference strategies. For example, individuals may specialize in a narrow range of environmental temperatures, concentrating fitness-enhancing activity in the limited periods of favorable conditions. Or they may evolve as generalists, active over a broad range of conditions. In this article, I use optimality models to explore the fitness costs and consequences of thermal specialization in variable environments.

Abiotic environmental factors, such as irradiance, temperature, salinity, and relative humidity, often exhibit some degree of predictable diurnal and seasonal variation. Physiological processes, on the other hand, often require quite specific and narrow physical conditions for efficient operation. In response to the constant selection pressure imposed by temporal variation, many species evolve behavioral and physiological homeostatic mechanisms. The buffering of internal operative conditions from external environmental fluctuation allows the evolution of specialized physiologies, presumably at some significant fitness benefit. However, for many species body size or habitat requirements do not allow even partial homeostasis, regardless of its potential advantages. Although the physiology of such organisms might in fact evolve to allow activity over a broad environmental range, fitness-enhancing activities such as growth and reproduction are often restricted to a narrow preferred range of conditions even in the most variable of environments (Andrewartha and Birch 1954). This range is often as narrow as that of species capable of internal regulation, even though such specialization may greatly reduce the proportion of the life span available for increasing fitness. The theory presented in this article seeks to identify the fitness consequences of adopting a specialized or generalized physiology under different patterns of temporal variation.

Realized fitness in a fluctuating environment depends on both tolerance (defined here as the probability of survival as a function of temperature) and performance, the capacity of an individual to grow, mate, and reproduce at various temperatures (Huey and Kingsolver 1989). Levins (1968) provides theory on the evolution of physiological tolerance in temporally varying environments. While constant environments obviously favor specialists, Levins concluded that a variable environment with two discrete states might favor either a monomorphic population of generalists or a polymorphic population of specialists. Levins, however, overestimated the mean fitness of specialists in heterogeneous environments: polymorphisms are unlikely to be maintained, and generalists, whose tolerance breadth spans the two environmental states, are the favored phenotype (Nagylaki 1975; Slatkin and Lande 1976). Recently, Lynch and Gabriel (1987) examined the influence of continuous within- and between-generation variation in the environment on the evolution of ecological tolerance. Again, temporal variation selects for generalists. The tolerance curve (the function describing survival rate along a continuous environmental gradient) should evolve to span the range of conditions an organism is likely to experience within a generation.

Levins (1968, p. 17) assumed that conclusions drawn from the study of tolerance curves would apply to the evolution of performance factors, such as growth, foraging, and reproduction. His models do not, however, predict the narrow preference ranges we often observe in nature. This failure results from ignoring

the differences in the calculation of fitness within each generation when considering survival rate versus reproductive success or growth (Levene 1953). In tolerance curve models, the fitness of an individual at time t is the product of its probabilities of survival in all previous time periods (Lynch and Gabriel 1987, p. 290). Growth and performance traits affecting reproduction contribute to lifetime fitness in an additive fashion under discrete generation models (Taylor 1981). Fitness at time t is the sum of fitness accumulated in all previous time periods. An episode in which the internal environment exceeds the critical limits of performance does not affect past or future fitness accumulation.

Here I examine the evolution of the preferred temperature range for performance traits in a cyclically varying thermal environment. I assume that the ability to successfully reproduce depends on encountering favorable environmental conditions and that the performance range will always be a subset of the temperatures within the tolerance range. I then explore how natural selection imposed by environmental variation on two timescales, within and among generations, shapes the fitness landscape. Several mathematical functions take these or other parameters to define the performance curve, a plot of performance as a function of temperature that depicts the degree of thermal sensitivity (Huey and Slatkin 1976; Huey and Kingsolver 1989). I will show that the optimal performance curve differs dramatically from the optimal tolerance curve in a changing environment. The results also illustrate the potential selective advantage of homeostasis. I model thermal sensitivity in this article because of the relative abundance of information about its ecological importance. The models, however, apply to any nonlinear physiological norm of reaction that describes the response of an organism to continuous environmental variation.

MODEL

Consider a small ectothermic insect with a short life span and several nonoverlapping generations a year. The model assumes a spring-summer growing season of 6 mo, with a dormant phase that is independent of the performance curve for the rest of the year. The model insect emerges as an adult at the start of the season and produces a new generation each 18 d, completing 10 generations each year. The adult life span is a uniform 5 d. Survival rate and performance of preadult life stages is random and uncorrelated with the adult traits considered here (see, e.g., Coyne et al. 1983).

I model reproductive success as a linear function of the rate of performance, with the performance rate determined by body temperature. For example, locomotory ability in ectotherms is often correlated with body temperature. A female's oviposition rate might be limited by her ability to locate and move among hosts (Messenger 1968; Kingsolver 1983a) or a male's probability of mating may depend on his running speed (Partridge et al. 1987). At different times during a day or a season, the instantaneous contribution of these acts to lifetime fitness will vary as a function of body temperature. A model performance curve illustrating the relation between performance and body temperature is shown in figure 1. Maximum performance (u_{\max}) and instantaneous reproductive success occur at the optimum temperature (T_{opt}). Performance breadth (T_{br}) is the difference between T_{\max} and T_{\min} , the maxi-

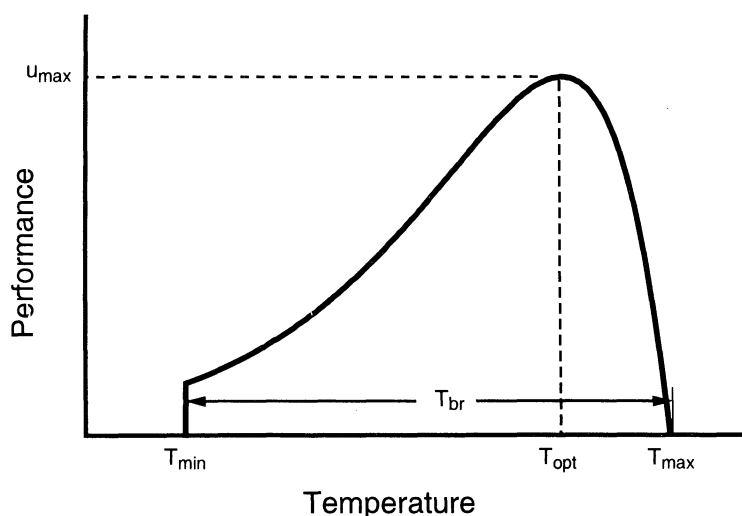


FIG. 1.—A thermal performance curve; T_{\min} and T_{\max} are the minimum and maximum temperatures at which performance is greater than zero, T_{opt} is the temperature at which the rate of performance is maximized (u_{\max}), and T_{br} is the difference between T_{\max} and T_{\min} . The curve was drawn using the Logan function (eq. [1]).

imum and minimum temperatures at which the performance rate is greater than zero. The model assumes that this temperature dependence is the only limitation on instantaneous fitness. Logic demands that the limits of performance lie within the tolerance range; beyond that, I have assumed that the traits are independent. If the proximity of the performance limits to the tolerance limits intensifies selection at the ends of the performance curve, narrower performance curves than those predicted by this model will be favored.

My performance models, like previous models of environmental tolerance (Levins 1968; Nagylaki 1975; Slatkin and Lande 1976; Lynch and Gabriel 1987), assume a constant area beneath the performance curve. The resulting trade-off between maximal performance and performance breadth (fig. 2) is often referred to as the “jack-of-all-trades is master of none” (Levins and MacArthur 1966; Levins 1968). A trade-off between generalists and specialists is often assumed in evolutionary ecology, but the data available to test the assumption are limited and frequently equivocal (Futuyma and Moreno 1988). I examine the consequences of relaxing this assumption later in the article. One consequence of the constant-area assumption for any model is that, as performance or tolerance breadth approaches zero, u_{\max} approaches infinity. I arbitrarily set $T_{\text{br}} = 1.0^{\circ}\text{C}$ as the minimum value possible.

I selected Logan et al.’s (1976) equation for insect temperature dependence to model the performance curve:

$$f(T_i, T_{\text{br}}, T_{\max}) = \Psi \{ e^{\rho(T_i - T_{\min})} - e^{[(\rho \cdot T_{\text{br}}) - 1.2\rho(T_{\max} - T_i)]} \}, \quad (1)$$

where

$$T_{\min} = T_{\max} - T_{\text{br}}. \quad (2)$$

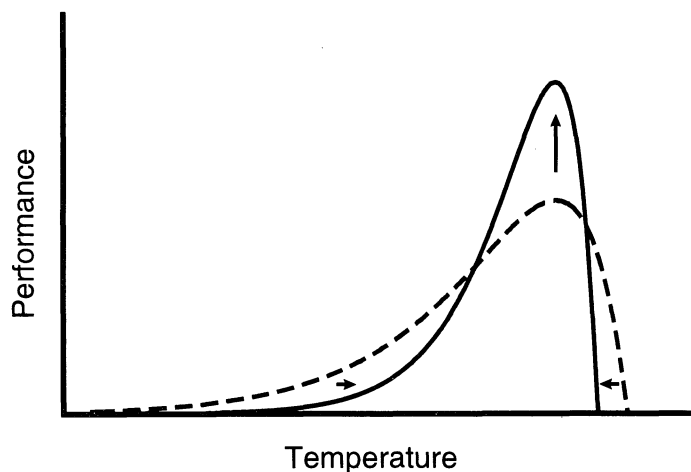


FIG. 2.—With a fixed area under the performance curve, the “jack-of-all-trades is master of none”; T_{br} and u_{max} are negatively correlated.

This function was used to construct the curves shown in figures 1 and 2. In the equations, T_i is the instantaneous body temperature. The constant Ψ determines the sharpness of the curve (a value of 4.0 was used throughout the models), and A is the area beneath the performance curve. This function provides a reasonably good fit with empirical measurements of temperature-dependent traits in insects, and the critical parameters ρ , T_{br} , and T_{max} are all biologically meaningful. In practice, entomologists have used this model to determine the accuracy of simple degree-day models of growth and development (Higley et al. 1986). Other performance curve functions can be used in place of the Logan model with similar results (see Results).

The trade-off between specialists and generalists is mediated by the parameter ρ , which corresponds roughly to the physiological parameter Q_{10} (the ratio of reaction or performance velocities at temperatures 10°C apart [Hochachka and Somero 1984]). For given values of T_{br} and Ψ , ρ is the constraint enforcing the constant area assumption. The area beneath the performance curve is obtained by integrating equation (1) with regard to T_i :

$$0 = \Psi \left[\frac{1}{\rho} (e^{\rho \cdot T_{br}} - 1.0) - \frac{0.8\bar{3}}{\rho} (e^{\rho \cdot T_{br}} - e^{-0.2\rho \cdot T_{br}}) \right] - A. \quad (3)$$

An algebraic expression for ρ cannot be obtained, so values of ρ were obtained using the VanWijngaarden-Dekker-Brent method for finding roots (Press et al. 1988).

The environment is modeled as a single continuous factor, temperature, that varies on both a daily and a seasonal cycle (fig. 3). Both unimodal and bimodal distributions of diurnal temperatures were considered. In the unimodal case, the daily temperature distribution is a truncated normal distribution (range: 0°–50°C) of 48 15-min time periods, with a specified standard deviation, σ . The seasonal

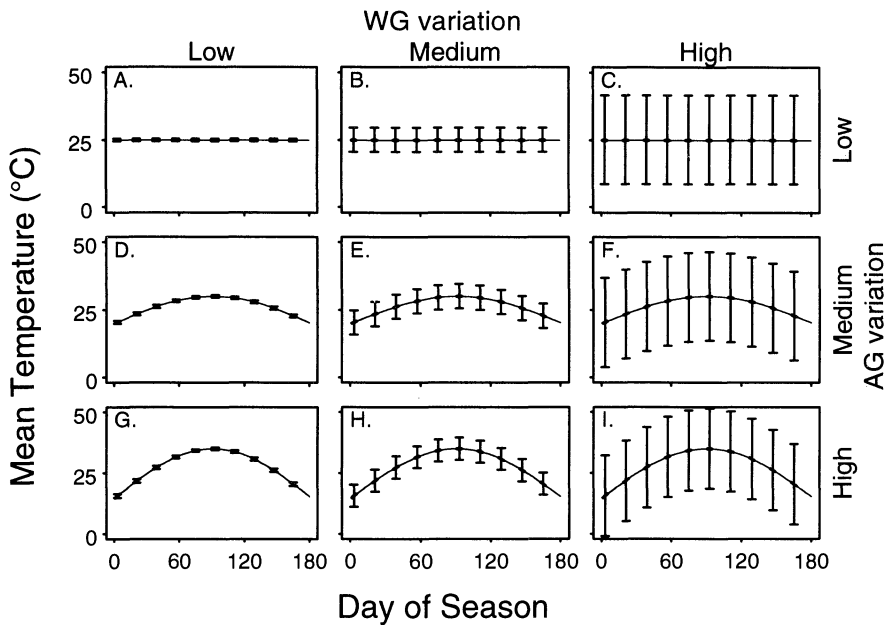


FIG. 3.—The modeled patterns of within- and among-generation (*WG* and *AG*, respectively) environmental variation over the course of a 180-d active season. The points denote the duration of each generation. The *WG* variation, represented by the error bars, is modeled as the standard deviation of the distribution of temperatures within a day; *AG* variation is modeled as a seasonal range of temperatures. See text for details.

change in mean temperatures is modeled as a sinusoidal trajectory with a periodicity of $2\pi = 360$ d (Curry and Feldman 1987). The daily mean is given by

$$\bar{T} = \delta \left[\sin \left(\text{date} \times \frac{\pi}{180} \right) - \frac{1}{2} \right] + 20, \quad (4)$$

where δ is the seasonal range of mean temperatures. The “active season” for the insects covers a 180-d period. The within-generation (*WG*) variation is described by the lifetime distribution of 240 time periods ($5 \text{ d} \times 48 \text{ time periods per day}$) at various temperatures; the among-generation (*AG*) variation is due to the variation in means among generations (fig. 3).

The simulations were run under all combinations of $\delta \in \{0.0, 10.0, 20.0\}$ and $\sigma \in \{0.5, 4.5, 16.5\}$. Since both seasonal and diurnal environmental variation in temperature tend to increase as one moves from the equator toward the poles (the diagonal from top left to lower right in fig. 3), special situations must be invoked to represent the other patterns of environmental variation. Large ponds and deep forests, for example, experience reduced levels of diurnal variation in temperature, although their seasonal fluctuations may be large in temperate climates (e.g., lower left in fig. 3). Annual species with a single generation each year may experience significant *WG* variation but relatively little *AG* change (e.g., upper right in fig. 3, but substituting a longer timescale on the *X*-axis).

Any environmental factor that follows an approximately sinusoidal trajectory through time will exhibit a bi- or trimodal distribution. Thus, diurnal patterns of temperature, irradiance levels, and humidity are usually bimodally distributed (Curry and Feldman 1987). I have explored the effects of a bimodal temperature distribution in two ways. In the first, I picked an intermediate distribution of temperatures about each mode ($\sigma = 4.5^\circ\text{C}$) and examined changes in the optima as the distance between the modes increased. The change in temperature distributions from high and low latitudes reflects a similar pattern. I then set a constant distance between the modes (10°C) and examined the effect of increasing the variance about each mode. This pattern is found when comparing the temperature distributions at high and low altitude. These models also extend the potential application to include environmental factors that lack a simple, continuous distribution. I modeled the bimodal environment as a mixture of two normal distributions sharing a common standard deviation and separated by an intermodal distance (IMD). Among-generation environmental variation follows a sinusoidal trajectory through time, as in the unimodal case.

Throughout this article, I assume that the organism is isothermal with the environment to simplify the bookkeeping in and explanation of the model. If thermoregulation confers independence from environmental temperatures, then body temperature can be substituted for environmental temperature with no loss of generality. The distribution of temperatures and the performance curve are combined to yield the fitness of phenotype i in generation g . The appropriate measure of phenotypic fitness in a fluctuating environment is the geometric mean over time (Haldane and Jayakar 1963):

$$\bar{W}_i = \left\{ \prod_{g=1}^n \left[\sum_{j=T_{\min}}^{T_{\max}} F_g(T_j) \cdot f(T_j, T_{\text{br}}, T_{\text{crit}}) \right] \right\}^{1/n}, \quad (5)$$

where $F_g(T_j)$ is the frequency of T_j within generation g and $f(T_j, T_{\text{br}}, T_{\text{crit}})$ is the fitness obtained within each time interval at T_j . For the Logan model, $T_{\text{crit}} = T_{\text{max}}$; for a Gaussian curve, $T_{\text{crit}} = T_{\text{opt}}$. The summation over the distribution of temperatures gives the lifetime fitness of a phenotype under some pattern of within-generation temperature variation. This computation ignores the potential complications imposed by diploid, sexual genetics; I thus assume clonal inheritance and an exact mapping of genotype onto phenotype. I could not obtain an analytical solution for equation (5), so I computed numerical solutions for all combinations of T_{br} from 1° to 30°C and T_{crit} from 10° to 50°C .

MODEL RESULTS

Unimodal Environments

I present the numerical solutions to equation (5) as fitness landscape contours (fig. 4). The height of the landscape is the geometric mean annual fitness for that phenotype (Haldane and Jayakar 1963). The nine plots in figure 4 correspond to the nine environments depicted in figure 3. A single optimum emerges in all cases

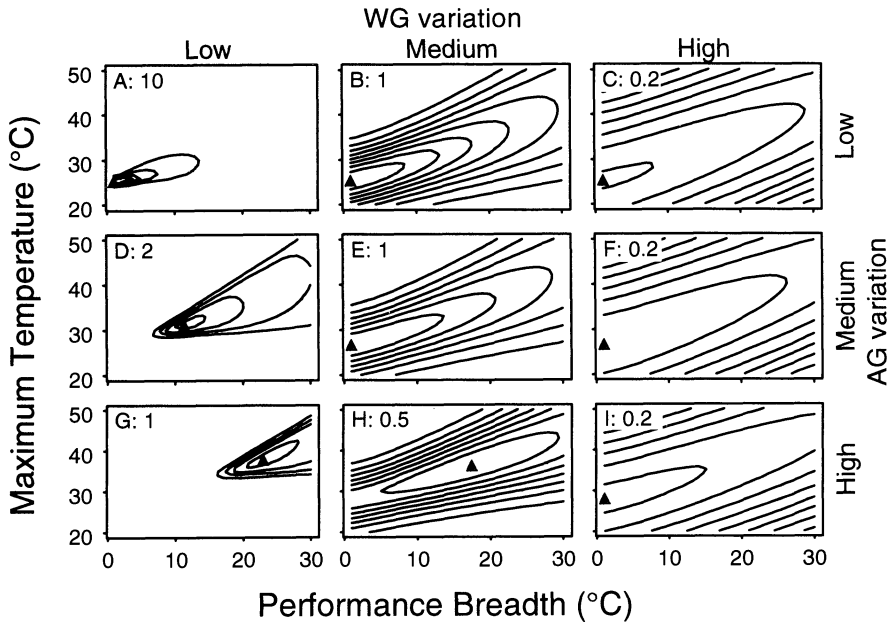


FIG. 4.—The fitness surface for each of the nine patterns on environmental variation shown in fig. 3. The height of the contours is fitness; the number to the right of each figure's letter is the interval, in arbitrary fitness units between contour lines. The triangle in each figure represents the location of the highest peak.

with specialization favored under most environmental scenarios. Selection within generations always favors specialists, with the steepness of the landscape inversely related to the degree of *WG* variation (fig. 4A–C). Increasing the *AG* component of environmental variation with little *WG* variation favors the evolution of generalists (fig. 4A, D, G). As *WG* variation increases, specialists are favored even in the face of considerable *AG* variation (fig. 4F, I).

The parameters of the optimal Logan curves in figure 4 are given in table 1 along with comparable parameters for two alternative performance curve models: a simple rectangle and a Gaussian curve. Performance and tolerance curves in nature are skewed to the left because of thermodynamic and enzymatic constraints (DeWitt and Friedman 1979; Huey and Kingsolver 1989), so symmetric functions such as Gaussian curves do not reflect biological reality. Optimal performance breadth is relatively independent of the performance curve function; however, the asymmetry of the curve affects its position along the environmental gradient, as indicated by variation among the models in T_{\max} or T_{opt} . Note that the geometric mean fitness of the optimal phenotype in a constant environment is an order of magnitude higher than the mean fitness of any phenotype in a more variable environment.

Assuming a constant area beneath the curve is a convenient way to model the specialist-generalist trade-off, but there is no a priori reason to expect such a

TABLE 1

PARAMETERS FOR OPTIMA OBTAINED THROUGH VARIOUS PERFORMANCE CURVE MODELS UNDER DIFFERENT PATTERNS OF WITHIN- AND AMONG-GENERATION VARIATION

AG AND WD (°C)	LOGAN					GAUSSIAN			RECTANGLE		
	T_{br} (°C)	ρ	T_{max} (°C)	T_{opt} (°C)	Fitness	T_{br} (°C)	T_{opt} (°C)	Fitness	T_{br} (°C)	T_{max} (°C)	Fitness
.0:											
.5	1.00	5.88	25.29	25.13	74.25	.25	25.00	78.61	1.00	25.50	68.27
4.5	1.00	5.88	25.30	25.15	8.86	.25	25.00	8.87	1.00	25.50	8.85
16.5	1.03	5.66	25.31	25.15	2.42	.25	25.00	2.75	1.00	25.50	2.42
10.0:											
.5	11.29	.26	31.23	27.72	9.06	3.06	26.37	7.76	10.32	30.32	9.08
4.5	1.01	5.80	26.65	26.49	6.97	.26	26.41	6.94	1.00	26.85	6.96
16.5	1.03	5.66	26.66	26.49	2.37	.25	26.05	2.73	1.00	26.85	2.37
20.0:											
.5	22.91	.09	37.94	28.04	4.40	6.23	27.71	3.87	20.92	35.56	4.89
4.5	17.38	.14	36.24	29.70	3.96	4.33	27.71	3.87	15.56	35.16	3.95
16.5	1.03	5.66	28.00	27.84	2.25	.25	27.95	2.66	1.00	28.19	2.25

NOTE.—Abbreviations are as follows: AG, among-generation variation; WG, within-generation variation; T_{br} , performance breadth; T_{max} , maximum temperature at which performance ceases; T_{opt} , temperature at which performance is maximal; ρ corresponds to a Q_{10} (see text for details). Fitness is given in arbitrary units. Note that performance breadth in the Logan and rectangular models refers to the range over which a nonzero level of performance is possible (minimum possible value = 1.0°C), whereas, in the Gaussian model, it corresponds to the width of the curve centered at T_{opt} and bounding ~68% of the total area under the curve (minimum possible value = 0.25°C).

specific, scale-dependent assumption might be common in nature. I relaxed the constant-area assumption in two ways. Under the “specialist advantage” model, I allowed the area beneath the curve to increase by 1% for each 1°C reduction in performance breadth. The “generalist advantage” model allowed the area to increase by 1% for each 1°C increase in performance breadth. In both cases, a performance breadth of 12°C was arbitrarily assigned a relative area of 1.0. The optimal performance breadths under the specialist-advantage model (table 2) are similar to those in the constant area case (table 1). The only noticeable change is at $WG = 4.5^\circ\text{C}$, $AG = 20.0^\circ\text{C}$, where performance breadth was 5°C narrower under the specialist-advantage model. Under the generalist-advantage model (table 2), optimal performance breadths increased dramatically in those environments where WG is large. In such cases, the flatness of the fitness landscape allows small fitness advantages to have a large effect on the location of the peak.

Bimodal Environments

The models presented above assume a unimodal distribution of temperatures within generations, but this is not the typical situation in nature. First, consider the case in which the intermodal distance of the environmental distribution is varied. When the IMD is small and the AG value low to moderate, there is a single peak in the fitness landscape: a curve with a narrow T_{br} and a T_{max} that places the performance optimum near the midpoint of the two modes (fig. 5A–B, D–E). As IMD increases, three peaks appear at low to moderate AG levels: the

TABLE 2
PEAKS ON THE FITNESS LANDSCAPE FOR DIFFERENT PATTERNS OF WITHIN- AND AMONG-GENERATION VARIATION

AG AND WG (°C)	SPECIALIST ADVANTAGE					GENERALIST ADVANTAGE				
	T_{br} (°C)	T_{max} (°C)	T_{opt} (°C)	Fitness	Relative Area	T_{br} (°C)	T_{max} (°C)	T_{opt} (°C)	Fitness	Relative Area
.0:										
.5	1.00	25.20	25.13	82.57	1.11	1.00	25.21	25.13	65.94	.89
4.5	1.00	25.22	25.14	9.83	1.11	3.84	26.06	25.64	7.98	.92
16.5	1.00	25.22	25.14	2.68	1.11	30.00	34.02	27.26	2.58	1.18
10.0:										
.5	11.16	29.40	27.71	9.13	1.01	11.55	29.49	27.70	9.01	1.00
4.5	1.00	26.56	26.49	7.73	1.11	6.63	28.29	27.44	6.38	.95
16.5	1.00	26.56	26.48	2.64	1.11	30.00	35.35	28.59	2.54	1.18
20.0:										
.5	22.14	32.45	27.54	3.89	.90	23.53	33.43	28.63	4.94	1.12
4.5	12.31	31.50	29.54	3.85	1.00	22.33	34.22	29.76	4.28	1.10
16.5	1.00	27.90	27.83	2.50	1.11	30.00	37.05	30.29	2.43	1.18

NOTE.—The area beneath the performance curve is negatively correlated with T_{br} under specialist advantage, whereas it is positively correlated with T_{br} under generalist advantage.

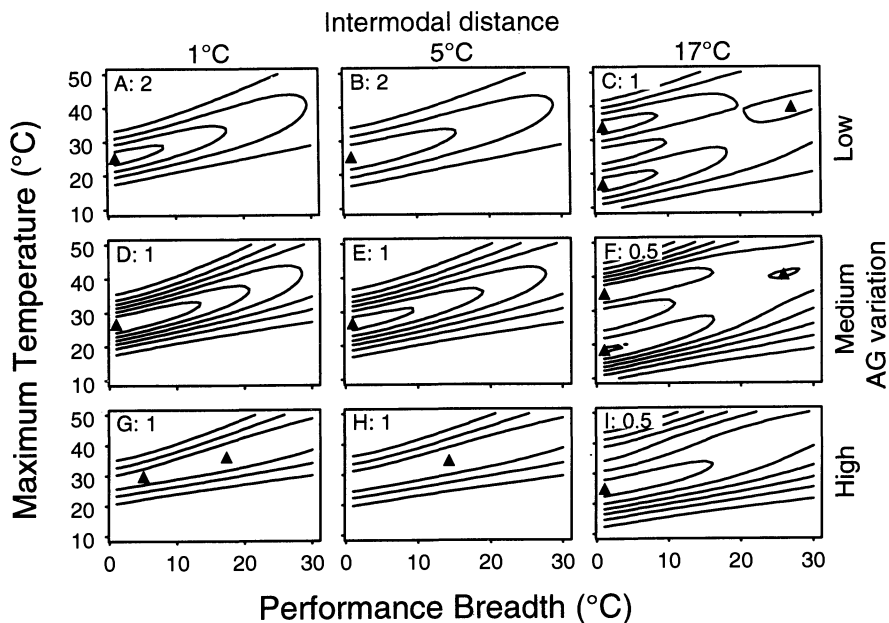


FIG. 5.—Fitness surfaces for a bimodal temperature distribution, with the intermodal distance varying between 1° and 17°C. The WG variation about each mode is $\sigma = 4.5^\circ\text{C}$.

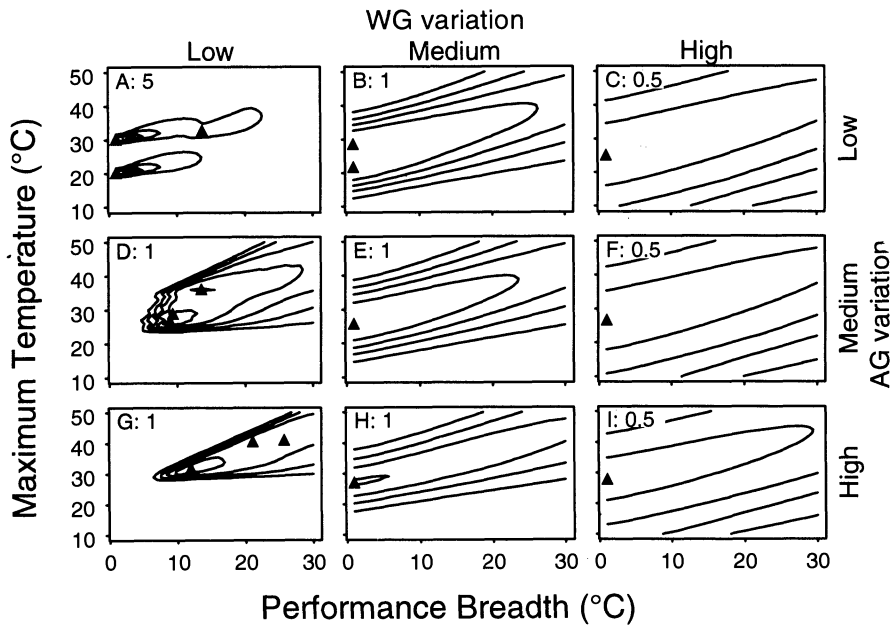


FIG. 6.—Fitness surfaces for a bimodal temperature distribution, with the WG variation about each mode increasing. The intermodal distance was held constant at 10°C.

two specialist phenotypes have equal fitness at their respective peaks, with a sizable advantage over the generalist (fig. 5C, F). The complex interaction between the intermodal distance and the within- and among-generation components of variation becomes apparent at the highest AG value. When the IMD is small, two peaks occur along a ridge of high fitness (fig. 5G); as IMD increases, a single peak emerges. At the greatest IMD (fig. 5I), the optimal phenotype is a specialist with a narrow performance curve lying between the two environmental modes.

Next, consider the case of a constant intermodal distance, in which the distribution of temperatures in each of the environmental modes varies (fig. 6). When AG variation is low, three peaks exist (fig. 6A): two specialists, each optimized for one environmental mode, and a generalist capable of exploiting both temporal “patches” but having a lower fitness than either specialist. As the AG component of variation increases, the interaction between environmental variation on different timescales produces a diverse array of optimal phenotypes (fig. 6D, G). As the variation increases about each mode (fig. 6, moving to the right), the multiple peaks disappear and specialist phenotypes predominate.

DISCUSSION

Environmental Variation and the Dominance of Specialist Strategies

The performance curve determines the amount of time an individual has to forage, grow, mate, and oviposit under a given pattern of temporal variation.

Natural selection favors increased efficiency during even limited times of optimal conditions rather than extending the range of conditions that support fitness-enhancing activity. The same specialist phenotype, characterized by a narrow T_{br} , is favored in both constant environments and in environments with substantial within- and among-generation variation (table 1; figs. 4–6). In a variable environment, specialization is made possible by the existence of some period of suitable conditions for mating, oviposition, and other fitness-related activity during the organism's lifetime. Specialists are favored if such a time window exists and if specializing on those conditions provides enough of an increase in efficiency during those times. Selection favors broad performance breadths only in environments characterized by considerable among-generation but little within-generation variation. In the absence of WG variation, the performance curve must encompass the full range of conditions seen by all generations. A single generation in which a phenotype encounters no suitable conditions for growth or reproduction results in extinction of that phenotype. Incorporating stochasticity about the daily and seasonal cycles in these models has no effect on the qualitative results presented here (G. W. Gilchrist, unpublished data).

The limited empirical data available suggest that narrow ranges of thermal preference seem to be the rule rather than the exception. Examples include growing larvae and ovipositing female insects (Harries 1939), fish (Beitinger and Fitzpatrick 1979; Reynolds and Casterlin 1979), and reptiles (Hertz et al. 1983; Huey and Bennett 1987). In many species of insects, females frequently fail to lay their full complement of eggs because of thermal restriction of flight activity (see, e.g., Burnett 1960; Stern and Smith 1960; Messenger 1968; Williams 1981; Jones 1987). Kingsolver (1983*b*) found dramatic evidence of environmental limits on flight time in *Colias* butterfly populations spanning a 2-km range of altitudes. Individuals in all populations have similar narrow flight performance ranges, requiring body temperatures of 30°–40°C, with vigorous flight restricted to the 35°–38°C range. Kingsolver estimated the mean number of hours per day available for flight at three different altitudes: *Colias philodice* at 1.7 km has 10.2 h, *Colias philodice* at 2.7 km has 3.4 h, and *Colias meadii* at 3.6 km has 2.9 h. The limitation on flight at high altitude causes a substantial reduction in time available for mating, foraging, and oviposition (Kingsolver 1983*a*). Few cases exist in which both tolerance and performance curves have been measured on a single population. The performance curves for growth rate and maximum daily egg production in *Drosophila melanogaster* have a narrow plateau from 24°–30°C (David and Clavel 1967, 1969), whereas the thermal tolerance curve is nearly rectangular, with a broad plateau extending from 14°–32°C (David and Clavel 1967). Anecdotally, thousands of species in essentially all phyla employ diapause, hibernation, or dormancy strategies to tolerate a very broad range of environmental conditions while restricting growth and reproduction to a specific season.

The models are insensitive the shape of the performance curve (table 1), but they are quite sensitive to variation in the trade-off function. The constant-area assumption used in this and in previous models of tolerance curve evolution forces the trade-off between T_{br} and u_{max} and is the most interesting case. Lifetime fitness is the product of the performance function and the frequency distribution

of temperatures, summed over the range of temperatures encountered during a generation (eq. [5]). For phenotypes near a fitness peak, lifetime fitness is directly proportional to the area of the performance curve; the consequences of deviations from the constant-area assumption follow logically. The fitness advantage shifts toward specialists if breadth and performance area are negatively correlated; if the correlation is positive, the advantage shifts toward generalists. The effect should be most apparent in environments with a large within-generation component of variation. Because the fitness surface flattens as the *WG* component of environmental variation increases, small increases in area with increasing T_{br} can shift the advantage from specialists to generalists.

The models predict that selection will favor similar performance breadths in populations from either constant or more variable environments; however, this prediction is also made by the hypothesis of phylogenetic inertia. These hypotheses can be tested by comparing the distribution of T_{br} and T_{max} among populations or species across a broad range of thermal habitats. The ridge in the fitness landscapes (figs. 4–6) implies that selection for changing T_{max} should produce a more rapid change than selection on T_{br} , all else being equal. If we assume that the populations are adapted to their thermal habitat, they should exhibit greater among-population variation in T_{max} than in T_{br} and a positive correlation between T_{max} and T_{br} . The hypothesis of phylogenetic inertia predicts that both T_{br} and T_{max} should be conserved and therefore should exhibit similar patterns of variation; this hypothesis makes no prediction about correlation.

While data for populations within a species are not available, one compilation of thermal sensitivity data for a range of species is available. Moore (1940) compiled data on the range of temperatures over which development is possible for 38 species of aquatic animals spanning five phyla and eight amphibious (one genus) or terrestrial animals (one genus). This small data set allows a comparison of the distributions of T_{br} and T_{max} and the estimation of the predicted positive correlation between T_{br} and T_{max} . I used the residuals from a nested ANOVA (model: trait = phyla + genus-in-phyla + error) to identify the level(s) at which evolution has or has not occurred in these traits. I compared the variances and correlation at the species level to test the hypotheses outlined above. The fitted values (model: trait = genus-in-phyla + error) allowed comparison of evolution at the genus level.

The variance of T_{br} is significantly lower than that of T_{max} at both the genus and the species level, and T_{br} and T_{max} are positively correlated at both taxonomic levels (table 3). Thus, maximum temperature limits are apparently more evolutionarily labile than development breadth, as suggested by the models. The data are also consistent with the predicted positive correlation between T_{br} and T_{max} . While the conservation of breadth could be entirely due to phylogenetic inertia, the higher variation in T_{max} suggests that the hypotheses of adaptive change predicted by the models cannot be rejected.

Limitations of the Models and Constraints on Performance Curve Evolution

These models define optimal solutions to the problem of adjusting performance to some range of environmental temperatures, under the assumption that fitness

TABLE 3
ANALYSIS OF DEVELOPMENT BREADTH DATA

Breadth	Variance	<i>F</i>	<i>r</i>
Species level	.96	.2318 (.0001)	.3482 (.0142)
Genus level	23.90	.5356 (.0328)	.7088 (.0001)

SOURCE.—Moore 1940.

NOTE.—The results show *F*-tests comparing variance in the traits at two different taxonomic levels and Pearson's product-moment correlations between the two traits; *P* values are given in parentheses. At the species level, $T_{\max} = 4.15$; at the genus level, $T_{\max} = 44.62$.

has a linear relation to performance (Huey and Slatkin 1976; Arnold 1983). The precise relation between performance and fitness across a range of environmental conditions is unknown for most organisms. It is a challenge to measure performance in the laboratory and relate it to fitness in the field (Bennett and Huey 1990). A few studies have demonstrated an approximately linear relation between locomotory performance and components of fitness. For example, several measures of locomotory performance were positively correlated with survival rate in a natural population of garter snakes (Jayne and Bennett 1990). In another study, the walking speeds of four strains of the parasitic wasp *Trichogramma maidis* predicted the relative rates of parasitism on the eggs of the moth *Ostrinia nubalis* (Bigler et al. 1988). The consequences of nonlinear fitness functions relating performance to fitness will depend on their particular form.

Optimality models provide information about how selection should act on a trait. The response to selection, however, is often limited by various constraints (Gould and Lewontin 1979; Maynard Smith et al. 1985; Wagner 1988). Limitations on adult performance may arise because of physiological acclimation or developmental responses to conditions experienced during earlier stages of life (Huey et al. 1995). Genetic constraints can also play a significant role in limiting evolution (Clark 1987; Scharloo 1987; Via 1987; Slatkin and Frank 1990). The optimal phenotypes cannot be reached if selection depletes genetic variation more rapidly than mutation restores it (Fisher 1958; Turelli 1984). Clearly, genetical models of performance curve evolution are needed to address these issues (G. W. Gilchrist, unpublished manuscript).

Finally, organisms are also subject to the laws of mechanics and physics, limiting the possible range of solutions. In a perfectly constant environment, the optimal locomotory performance curve would be infinitely narrow and infinitely high at the precise temperature of the environment. In reality, mechanical constraints on muscular and skeletal components, kinematic constraints on metabolic processes, and energetic constraints on whole-animal metabolism will limit the range of solutions and may impose an upper limit on performance. Because of these limitations, selection will rarely be strong enough to favor the extremely narrow performance curves predicted by the models. A more realistic expectation is that the performance breadths of real organisms will generally be narrower than the range of environmental conditions experienced within any one generation.

Ecological and Evolutionary Significance of Specialization in Variable Environments

Animals capable of homeostatic control of temperature, pH, salinity, and other physical factors within the body gain access to resources at times when environmental conditions prevent environmental conformers from being active. The metabolic cost of endothermy is estimated at about 10 times the cost of thermoconformity, with benefits including increased stamina and aerobic capacity (Bennett and Ruben 1979). In the context of this model, a homeotherm is essentially a specialist in a constant environment (fig. 4A). The quantitative fitness advantage over thermoconformers in a variable environment is immediately apparent: the specialist in a constant environment has nearly a 10-fold increase in fitness over any other phenotype under any pattern of environmental variation (table 1). The models suggest that apparently costly mechanisms of behavioral thermoregulation as well as endothermy have the potential to greatly increase fitness (Huey and Stevenson 1979).

Temperature and light follow a bi- or trimodal distribution during the course of a day, creating the opportunity for multiple environmental niches under some patterns of temporal variation (figs. 5, 6). The strong advantage of specializing reproduction on one of the environmental modes provides the disruptive selection needed to maintain genetic polymorphism in the face of temporal variation (Felsenstein 1976; Hedrick et al. 1976; Hedrick 1986). A population whose mating activity is confined to one of these discrete temporal niches is reproductively isolated from other populations, even in sympatry. The situation is similar to the spatial isolation of insect host races, in which disruptive selection arises through specialization on different host plants (Jaenike 1990). A few examples of polymorphism in thermal preference within insect populations appear in the literature. For example, individuals in a laboratory colony of the chalcid wasp, *Microplectreon fuscipennis*, may have preferences for temperatures of 22°–27°C, 15°–17°C, or 5°–7°C (Wilkes 1942).

Multiple niches and the flatness of the landscape in the face of *WG* variation imply that many phenotypes will have nearly equal fitness (figs. 4–6). Ecological factors such as competition or avoidance of predation may play a large role in determining the evolution of the performance curve in a highly variable environment. Sympatric species with similar ecologies could specialize in different temperature niches at little cost, thereby minimizing direct competition for resources. Sympatric populations of *Drosophila melanogaster* and *Drosophila simulans* differ in thermal optima. In laboratory competition experiments, *D. simulans* displaces *D. melanogaster* at 15°–20°C, whereas *D. melanogaster* consistently dominates at 25°C (Moore 1952; Tantawy and Soliman 1967). Similar shifts in thermal optima, with correlated shifts in competitive ability, have been observed in the grain beetles *Calandra oryzae* and *Rhizopertha dominica* (Birch 1953) and in Park's (1954) well-known experiments with *Tribolium* spp.

These models of performance curve evolution suggest a quite different scenario than the one depicted in models of tolerance curve evolution (Levins 1968; Nagylaki 1975; Slatkin and Lande 1976; Lynch and Gabriel 1987). In the most sophisti-

cated of these models, Lynch and Gabriel (1987) found that the tolerance range evolved to span the range of conditions that the organism was likely to encounter in its lifetime; increasing among-generation variation had relatively little effect. In the model presented here, increasing within-generation variation flattens the fitness landscape, while among-generation variation favors the evolution of broad tolerance ranges. Most important, the interaction between these components of environmental variation allows the evolution of narrow performance curves in variable environments. Taken together, the results of the performance and tolerance models suggest that, for most patterns of environmental variation, organisms should be "performance specialists" and "tolerance generalists." I think that most biologists intuitively recognize this to be the case. Data detailing the genetic correlations between these two important components of niche dimension are needed to further our understanding of evolution in changing environments.

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