EVOLUTION OF RESISTANCE TO HIGH TEMPERATURE IN ECTOTHERMS

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Abstract.—Body temperature influences the performance and fitness of ectotherms. How thermal sensitivity responds to selection for resistance to high temperature is broadly relevant in evolutionary physiology and also has practical implications. We review several complementary approaches to studying the evolution of thermal sensitivity. First, we analyze comparative data that illustrate the historical evolution of thermal sensitivity of locomotion in iguanid lizards. Taxa that experience high body temperatures in nature have evolved high optimal temperatures for sprinting. Critical thermal maxima are coadapted with optimal temperatures but not with critical thermal minima. Thus some but not all aspects of thermal sensitivity are coadapted. Second, we describe selection experiments that help reveal potential genetic constraints on the future evolution of thermal sensitivity in *Drosophila*. Thermal sensitivity responds rapidly both to laboratory natural selection and artificial selection, and tolerance of extreme high temperature appears genetically correlated with performance at intermediate temperature. Third, applying a recent model by Lynch and Lande, we describe how the shape of thermal performance curves may affect evolutionary responses of thermal sensitivity to a gradual shift in the thermal environment. Our theoretical predictions depend crucially on the relationship between the genetic variation in optimal temperature and the performance breadth. If genetic variation is independent of breadth, then populations with an intermediate value of performance breadth will tolerate the greatest rate of environmental change. Moreover, if a trade-off exists between maximum performance and breadth of performance, then thermal specialists will be favored over thermal generalists in a rapidly changing environment. On the other hand, if genetic variation increases with increasing breadth, then populations of thermal generalists will tolerate the greatest rates of environmental change.

Both the performance and fitness of ectotherms (e.g., microorganisms, insects, fishes, reptiles) are profoundly affected by body temperature. Performance or fitness typically increases with temperature, plateaus at an "optimal" or maximum level, and then declines precipitously near the upper critical or lethal temperature (fig. 1). Performance curves can be characterized quantitatively either by estimating various descriptive statistics (e.g., optimal or maximum performance temperature, performance breadth; fig. 1; Huey and Stevenson 1979) that summarize the shape and position of the performance curve or as "infinite-dimensional" statistics recently developed for complex traits such as growth trajectories, reaction norms, and performance curves (Kirkpatrick and Heckman 1989; Kirkparick et al. 1990).

How the shape and position of thermal performance curves evolve in response to selection has been the subject of considerable research (Huey and Kingsolver 1989). One of the basic issues is visualized in figure 2*a*. Imagine a hypothetical

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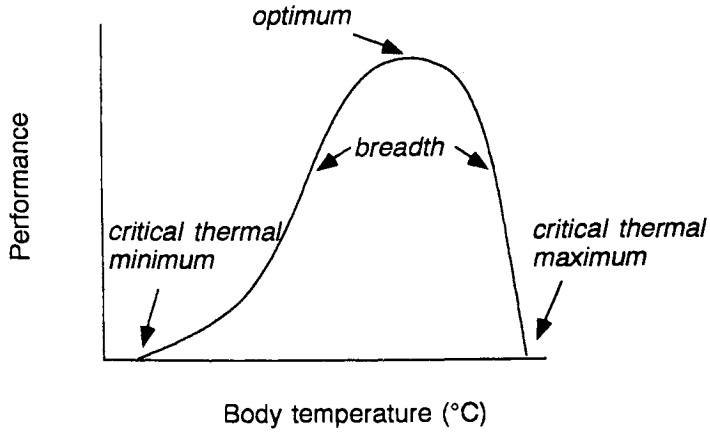

FIG. 1.—Effect of body temperature on the performance (fitness) of an ectotherm. (Redrawn from Huey and Stevenson 1979.)

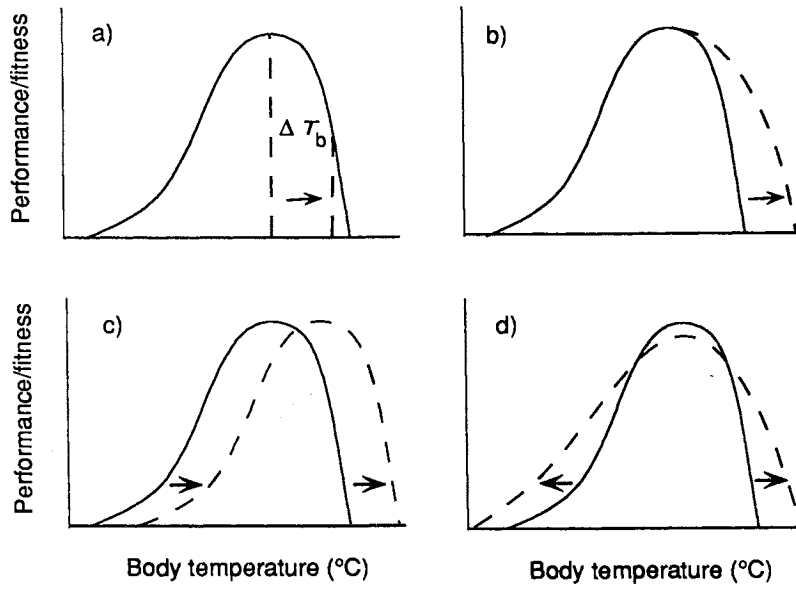

FIG. 2.—Possible evolutionary shifts in thermal sensitivity in response to selection for increased performance at high temperature. *a*, Performance curve for a hypothetical ectotherm that was initially active at its optimal temperature. With climate change, however, the population experiences higher body temperatures (ΔT_b) that reduce average performance, thus selecting for enhanced performance at high body temperatures. *b*, Hypothetical response (increased performance breadth; shown as *dashed curve*) to selection for enhanced performance at high temperature if no genetic correlation exists between performance at high vs. low temperature. *c*, Response to selection (shift of entire performance curve to the right) if performance at low and at high temperatures are inversely correlated. *d*, Response if selection for enhanced performance at high temperature also enhances performance at low temperature (stress resistance hypothesis), if a trade-off between maximum performance and breadth of performance is assumed.

population that is normally active at body temperatures that maximize performance and fitness. However, if the population begins to experience increased body temperature, either because of short-term shifts in habitat or weather or because of long-term shifts in climate, then its average performance will be reduced, which ultimately will lead to selection for an evolutionary shift in thermal sensitivity to restore performance levels (Huey and Kingsolver 1989). However, the evolutionary response of performance curves to such selection is not yet adequately resolved (Huey and Kingsolver 1989; Lenski and Bennett 1993). Several key issues require attention.

First, what is the maximum rate of environmental change that can be accommodated via parallel evolutionary shifts in thermal sensitivity? Because of the prospect of global warming (Schneider 1993), this issue has recently gained practical significance (Holt 1990; Hoffmann and Blows 1993). For example, consider a population in which average body temperature increases above optimal levels because of sustained climate warming (e.g., fig. 2*a*). Will the population have the genetic capacity to shift its thermal sensitivity quickly enough to track (and thus tolerate) this climate warming? Or will its thermal sensitivity lag behind the changing thermal environment, such that the population is eventually driven to extinction? What factors influence the rate of evolutionary shift in thermal sensitivity? For example, is genetic variation adequate for a strong response to selection? Do thermal performance breadths (fig. 1) influence the lag of thermal sensitivity behind the changing thermal environment as well as the maximum rate of tolerable environmental change?

Second, how does the shape of the performance curve itself respond to selection for increased resistance to high temperature (fig. 2*a*)? Several consequences are possible, depending on the genetic architecture underlying the shape of the performance curve (specifically, on whether resistance to high temperature is genetically correlated with performance at other temperatures). For example, if performance at high temperature is genetically independent of performance at low temperature, the performance curve might evolve largely by increasing breadth (fig. 2*b*). Alternatively, if performance at high and at low temperatures are genetically and inversely coupled, then selection might shift the entire performance curve to the right (fig. 2*c*). Finally, if the Parsons-Hoffmann model of "stress-resistant" genotypes holds (Hoffmann and Parsons 1989; Parsons 1990; Hoffmann and Parsons 1991), then selection for enhanced heat resistance will increase both heat and cold tolerance (fig. 2*d*). Moreover, if breadth of performance and maximum performance are inversely related because of a trade-off ("jack-of-all-temperatures is a master of none": Huey and Hertz 1984; Lenski and Bennett 1993), then maximum performance might be reduced.

In this article we summarize some of the evidence germane to the above two issues. We make no attempt to be comprehensive or encyclopedic; rather, we highlight a few of the approaches that we are currently using to address these issues. In particular we want to describe and contrast benefits and limits of three different approaches: a comparative-phylogenetic approach, studies of evolution in the laboratory, and theoretical models of the evolution of thermal sensitivity. Comparative studies provide information on the historical patterns of evolution

that have actually occurred. Studies of evolution in the laboratory quantify the magnitude of genetic constraints (heritabilities, genetic correlations) that might influence future responses to specified selection regimes. Theoretical models identify key variables that may be relevant to predicting responses to selection, and they can also inspire novel experiments. This multiperspective approach is rather eclectic, but intentionally so. Indeed, all three of these perspectives, as well as related perspectives (e.g., natural selection in the wild on thermal sensitivity, mechanistic bases of thermal sensitivity; Feder 1987; Bennett and Huey 1990; Garland and Adolph 1991), are complementary and provide crucial insights.

COMPARATIVE (PHYLOGENETIC) PATTERNS

Comparative data provide opportunities to reconstruct the historical changes that led to contemporary patterns (Felsenstein 1985; Huey and Bennett 1986, 1987; Brooks and McLennan 1991; Harvey and Pagel 1991; Harvey and Purvis 1991; Martins and Garland 1991; Garland et al. 1992). For example, comparative physiological data on contemporary species enable one to infer whether lineages that encountered warmer body temperatures in the past—perhaps from climate warming or from habitat shift—actually evolved increased tolerance of high temperature (Huey and Bennett 1987; Garland et al. 1991).

A traditional comparative approach to studying patterns of correlated trait evolution proceeds by measuring two or more traits in a variety of populations or species and then computing correlation coefficients between pairs of traits (reviewed in Harvey and Pagel 1991). To understand how such contemporary data can be used to elucidate historical patterns, consider a hypothetical lineage that was initially active at physiologically optimal body temperatures (fig. 2*a*) but that begins to experience climate warming and is thus forced to be active at body temperatures above optimal levels (Dunham 1993). If the resultant decline in performance has important negative effects on fitness (Christian and Tracy 1981; Arnold 1983; Jayne and Bennett 1990), then selection will favor a shift in the performance curve, specifically enhancing performance at high body temperatures. If this scenario is projected forward over evolutionary time, then the optimal temperature of different species should be positively correlated with average body temperature of that species (Huey and Bennett 1987). Moreover, if genetic correlations influence the evolution of performance curves (fig. 2), then correlated shifts should be detectable in other parts of the performance curve (e.g., a change in tolerance of low temperature). Such correlations involving interspecific or interpopulational data can be referred to as "evolutionary correlations" (Martins and Garland 1991).

To test these hypotheses, we examine comparative data to address several hypotheses on the thermal dependence of sprint speed in some iguanid lizards. Do species that have relatively high body temperatures also have relatively high optimal temperatures (or critical temperatures)? Do species that have relatively high upper critical and optimal temperatures also have relatively high (or low) lower critical temperatures, which could occur if a tight genetic coupling existed

between these traits? Although numerous studies address these and related issues in diverse taxa (e.g., fish: Brett 1970; *Drosophila:* David et al. 1983; Hoffmann and Parsons 1991; reptiles: Huey 1982), only one set of studies (Huey and Bennett 1987; Garland et al. 1991) has been conducted in an explicitly phylogenetic context (see below).

Data and Analyses

We analyze comparative data on the thermal dependence of sprint speed of 19 species of iguanid lizards. This analysis is part of a much larger study (R. B. Huey, A. F. Bennett, T. Garland, P. E. Hertz, and F. M. van Berkum, unpublished manuscript) of the evolution of the thermal dependence of sprint speed in over 60 species of lizards from many families.

To obtain the basic data for the present analysis, we (or our colleagues) measured the sprint speed for individuals of several species at a variety of body temperatures (Bennett 1980; Crowley 1985; van Berkum 1986, 1988; Huey et al. 1990; R. B. Huey, unpublished data). From these data we can readily estimate (van Berkum 1986) relevant descriptive statistics (fig. 1; e.g., optimal temperature for sprinting). (These studies were done on animals that usually had been acclimated for less than 2 wk. Although some of the differences undoubtedly reflect phenotypic plasticity, the magnitude of the interspecific differences [below] are much larger than have been observed in acclimation studies [e.g., van Berkum 1986] and thus reflect genetic differences.) We also extract field data on mean body temperatures of animals active in nature from the above references.

These basic comparative data enable us to search for evolutionary correlations between pairs of traits (e.g., between field and optimal temperatures). However, conventional correlational tests are inappropriate here because data from related species are not statistically independent (Felsenstein 1985; Harvey and Pagel 1991; Martins and Garland 1991) and therefore the degrees of freedom are inflated artificially (Martins and Garland 1991). Consequently, we used Felsenstein's (1985) method of standardized independent contrasts. This method computes a set of contrasts (differences or "contrasts" in trait values between two taxa) that are statistically independent of all other such contrasts and then computes correlation coefficients using these contrasts rather than the original trait values themselves (Garland et al. 1992). Felsenstein's method produces robust estimates of correlation coefficients (Martins and Garland 1991). However, it requires information not only on trait values themselves but also on the phylogenetic branching pattern and on branch lengths (expressed as units of expected variance of change for each character). The phylogeny for the iguanids is not settled, but we followed a phylogeny based primarily on the work of Frost and Etheridge (1989). Because actual branch lengths are unknown, we established arbitrary branch lengths by fixing the total length of all complete branches (i.e., the length from basal node to each tip) as equivalent to the maximum number of branches on any main branch (Pagel 1992). (In the present case these arbitrary branch lengths adequately standardize the independent contrasts [T. Garland, Jr., personal communication; see Garland et al. 1992.])

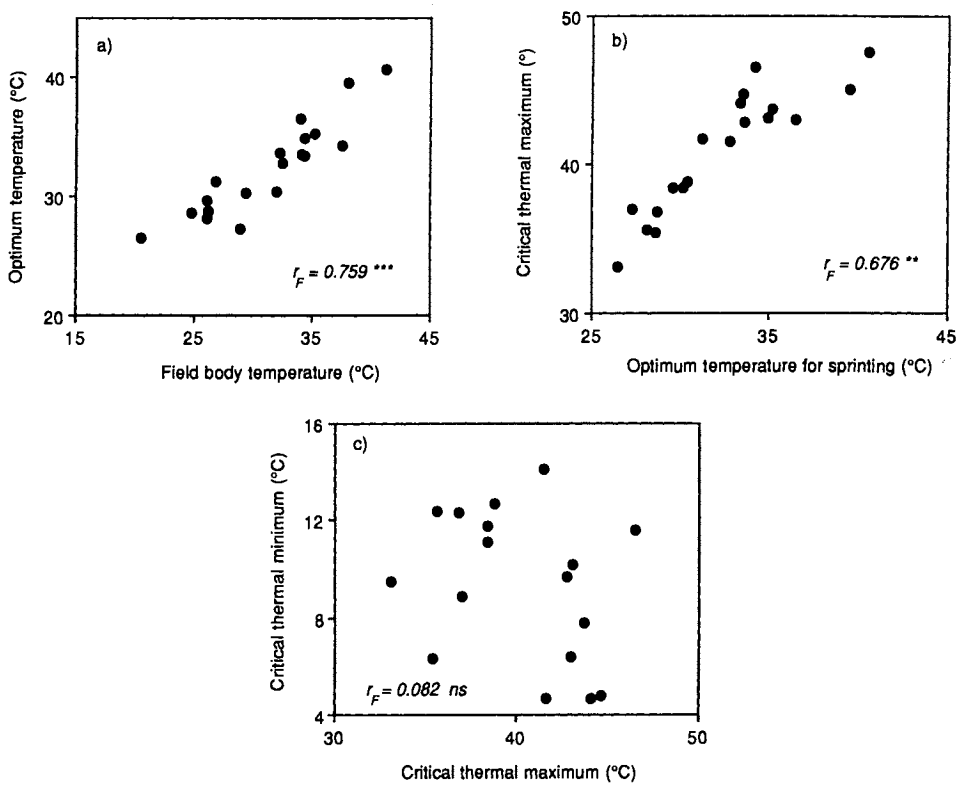

FIG. 3.—Evolutionary correlations involving 19 species of iguanid lizards. *a*, Optimal temperature for sprinting is positively correlated (r_F = Felsenstein's [1985] correlation coefficient for standardized independent contrasts; see text) with the average body temperature of lizards in the field; *b*, optimal temperature is positively correlated with critical thermal maximum; *c*, critical thermal maxima and minima are not significantly correlated.

Results

Iguanid species vary considerably (range = 15°C) in their optimal temperature for sprinting (fig. 3*a*). The mean optimal temperature for a given species is closely correlated with the mean body temperature experienced by those species in nature (fig. 3*a;* correlation for standardized independent contrasts = $r_F = 0.759$, $P < .001$). Thus thermal performance curves have clearly shifted during the evolution of the iguanid lizards, and the thermal dependence of performance is evolutionarily correlated with the mean activity temperature of species. Were the direction (i.e., ancestral vs. derived) of evolution at issue here, phylogenetic techniques could also be used to estimate those directional changes (Huey and Bennett 1987; Brooks and McClennan 1991; Harvey and Pagel 1991; Martins and Garland 1991).

Given this pattern we may next ask, Is an evolutionary shift in the optimal temperature correlated with a shift in the critical thermal maximum (fig. 1)? Yes, species that run fastest at high temperature also tolerate high temperatures (fig. 3*b;* $r_F = 0.676$, $P < .01$).

Finally, are the critical thermal maximum and minimum temperatures correlated evolutionarily? The answer is clearly no (fig. 3*c*; $r_F = 0.082$, $P > .5$). The critical thermal maximum and minimum temperatures seemingly evolve independently of each other.

Conclusions

Our findings can be compared with those of a previous study (Huey and Bennett 1987; Garland et al. 1991) that developed a phylogenetic analysis of the evolution of thermal sensitivity in 12 species of Australian lizards (Scincidae). The patterns in both studies are similar in direction, though fewer correlations (e.g., field body vs. optimal temperature, optimal vs. critical thermal maxima) were statistically significant in the smaller-scale skink study (Garland et al. 1991).

These phylogenetic patterns provide insights into historical changes in thermal performance curves. First, field body temperatures among species are evolutionarily correlated with changes in thermal sensitivity of lizard sprint speed. Clearly, heritable variation in iguanids has been sufficient for evolutionary shifts to occur, at least over long time periods. Second, optimal temperatures and critical thermal maxima tend to evolve together in the same direction. Two interpretations are possible. This evolutionary correlation might be indicative of an underlying genetic correlation that persists in different species or, alternatively, of an environmental correlation between the factors that selected independently on the two traits (Felsenstein 1988; Huey et al. 1991; Martins and Garland 1991). Third, the critical thermal maximum and minimum seemingly evolved independently, contrary to the hypothesis of a positive genetic correlation (Bradley 1982; Huey and Kingsolver 1989) and contrary to the generalized stress resistance hypothesis (Hoffmann and Parsons 1989, 1991).

SELECTION EXPERIMENTS

We now turn from the past to the present. In so doing, we do not ignore the past; rather, we use the above historical patterns to suggest hypotheses concerning how contemporary populations might respond to directional selection for enhanced performance at high temperatures, as might occur from global warming. Although the past is often used as a guide to the future, history can sometimes be a misleading predictor of future evolution. First, the underlying genetic architecture (e.g., linkage, mutational input, genetic correlations) can change over evolutionary time (Barton and Turelli 1989). Second, the nature of selection in the past might be different from that in the present. For example, global warming during the next century may proceed much faster than has ever occurred previously (Schneider 1993). Third, comparative data of extant species necessarily reflect only evolutionary success stories: extinct taxa, which may not be a random sample of a given clade, are not represented. Consequently, although historical patterns may suggest hypotheses of future evolution, their utility as a basis for policy decisions would seem somewhat tenuous.

Given these inherent limitations in comparative data (see also Huey and Bennett 1986), alternative approaches are required to test whether contemporary

populations will respond to selection on thermal sensitivity in ways predicted by comparative analyses. One powerful approach for testing evolutionary hypotheses involves conducting laboratory selection experiments and then observing the direct and correlated responses (Stearns 1989; Rose et al. 1990; Hoffmann and Parsons 1991; Hoffmann and Blows 1993). For example, one could select on critical thermal maximum and determine whether the critical thermal minimum is unaffected, as suggested by the above comparative data.

We use two types of general selection protocols with *Drosophila* (Rose et al. 1990). In "laboratory natural selection," a large laboratory stock is subdivided, and sublines are transferred abruptly to population cages with differing environments (e.g., temperatures, humidities, densities) and then left in those environments for multiple generations. Consequently, the stocks themselves evolve by natural selection, much as they might do in nature in response to an acute environmental change. (This is the same general protocol that Lenski and Bennett [1993] are using to study thermal evolution in *Escherichia coli*.) This protocol is efficient: individuals need not be measured, and populations can be large. Nevertheless, the experimenter does not control which phenotypes survive and breed, and thus the targets of selection are usually ambiguous (Rose et al. 1990).

A second approach is often called "artificial selection" (Rose et al. 1990). Here the experimenter first measures all individuals for a trait and then allows only certain phenotypes (e.g., the biggest or most heat tolerant) to breed. Thus the experimenter directly controls the targets of selection and can usually distinguish direct from correlated evolutionary responses. Of course, inadvertent selection on correlated traits can confuse these issues (Clark 1987).

Both types of selection experiments are complementary (Rose et al. 1990) ways of identifying genetic constraints on trait evolution. Of course, the genetic architecture underlying traits can alternatively be identified by using quantitative-genetic breeding designs (Clark 1987; Falconer 1989). A breeding design can have two clear advantages over selection approaches: it can be completed in fewer generations, and it directly estimates heritabilities and genetic correlations among *all* traits, not just those involving the selected character. Tools for describing the quantitative genetics of complex traits such as thermal performance curves are now available (Kirkpatrick and Heckman 1989; Kirkpatrick et al. 1990). Nevertheless, selection experiments have compelling counteradvantages for our purposes (see Clark 1987; Stearns 1989). First, selection experiments measure both direct and correlated evolutionary responses to selection, whereas breeding designs only predict (sometimes incorrectly) those responses (Clark 1987; te Velde and Scharloo 1988; Barton and Turelli 1989; Stearns 1989; Charlesworth 1990; Houle 1991). Second, selection experiments are powerful tools for studying the mechanistic bases of physiological evolution because they magnify physiological differences (i.e., signal:noise) between selected and control lines (Service et al. 1985; te Velde and Scharloo 1988; Graves et al. 1992). Third, selected lines (if maintained) can be used in post-factum studies (e.g., those involving traits that were not anticipated at the beginning of a study). With quantitative-genetic approaches, analysis of such traits would be possible only by redoing the basic breeding design and incorporating measurements of any new traits.

TABLE 1

DEVELOPMENT TIME VERSUS TEMPERATURE OF SELECTED LINES OF *DROSOPHILA*

DEVELOPMENT TEMPERATURE (°C)	SELECTION REGIME (°C)	MEAN DEVELOPMENT TIME* (d)	
		Females	Males
16.5	16.5	23.0 ± .02	23.6 ± .02
16.5	25	23.5 ± .02	24.3 ± .02
25	16.5	9.5 ± .02	9.7 ± .02
25	25	9.3 ± .02	9.6 ± .02

NOTE.—Data for *Drosophila melanogaster* from Huey et al. (1991).

* Point estimates corrected for density of mean (± SE) development times of three replicates per line per developmental temperature.

Natural Selection in the Laboratory

Several years ago a study of the laboratory evolution of thermal sensitivity of *Drosophila melanogaster* was begun (R. B. Huey and L. Partridge). In 1985, L. Partridge took a stock of flies that had originally been collected in 1984 in Brighton, England, and maintained them in population cages at 25°C for about 1 yr. Then she subdivided the stock and established lines of flies at either 16.5° ("low" temperature) or 25°C ("intermediate" temperature), with three replicate populations per line. She has maintained those lines ever since. In effect these flies have been subject to natural selection in the laboratory for growth and reproduction at low versus intermediate temperature. (These temperatures are within the limits of temperatures experienced by *D. melanogaster* in nature [Jones et al. 1987].) In the spring and summer of 1989, we (Huey et al. 1991) compared some aspects of the thermal sensitivity of the low- and intermediate-temperature lines. The findings are summarized here.

Did the 16.5° and 25°C flies diverge in thermal sensitivity between 1985 and 1989? If so, this would imply that significant heritable variation exists for thermal sensitivity (Stephanou and Alahiotis 1983). Moreover, did natural selection on performance at these nonextreme temperatures result in a correlated shift in tolerance to extreme high temperature? If so, this would imply a genetic correlation between performance at nonextreme temperatures (16.5°C, 25°C) and tolerance of extreme temperatures (39.5°C; see below).

We compared the lines for thermal sensitivity of development time (egg to adult). Time to maturity is of course highly temperature sensitive, with development being retarded at low temperature (David and Clavel 1967). Point estimates (correcting for density) of development time for females and males from the two lines at 16.5° and at 25°C are shown in table 1. At a low development temperature, the 16.5°C line develops faster than does the high-temperature line; but at a high development temperature, the reverse is true. (L. Partridge, B. Barrie, and V. French [personal communication] have repeated this experiment [with improved density control] and obtained similar results.) In other words, a significant line-by-temperature interaction ($P < .001$) has evolved in about 4 yr, which corresponds

TABLE 2

PERCENTAGE SURVIVAL OF ACUTE HEAT SHOCK OF SELECTED LINES OF *DROSOPHILA*

SELECTION REGIME (°C)	PERCENTAGE SURVIVING HEAT SHOCK*	
	Males	Females
16.5	7.1 ± .89 (3.7–13.1)	36.4 ± 1.74 (29.4–40.6)
25	9.9 ± 1.10 (6.9–14.6)	40.4 ± 1.85 (35.5–47.4)

NOTE.—Data for *Drosophila melanogaster* from Huey et al. (1991).

* Percentage of flies (mean ± SE [range] for three replicates) of selected lines that survived an acute heat shock (39.5°C for 30 min).

to fewer than 110 generations at 25°C or fewer than 66 generations at 16.5°C (Huey et al. 1991). So *Drosophila* clearly have the genetic potential for rapid evolution in thermal sensitivity when maintained at different (fixed) body temperatures (Stephanou and Alahiotis 1983; Cavicchi et al. 1989).

We also compared the lines for tolerance of an extreme heat shock. If the lines had diverged in heat tolerance, a genetic correlation would exist between performance at intermediate temperature and tolerance of extreme temperature. Recall that the lizard data (fig. 3*b*) suggested a potential genetic correlation between the optimal temperature and the critical thermal maximum. Flies from the high-temperature line have significantly higher survival of an acute heat shock (39.5°C for 30 min) than do flies from the low-temperature line (table 2; logistic regression, $P < .05$; Huey et al. 1991), which demonstrates that a genetic correlation does exist. However, the average differences between lines are minor, both absolutely and relative to the within-line variation (table 2). Even so, these results suggest that natural selection on performance at intermediate temperatures can influence the evolution of performance at extreme temperature, a pattern found previously by Stephanou and Alahiotis (1983). However, this result differs from that of Lenski and Bennett (1993), who found that natural selection at different temperatures generally resulted in temperature-specific increases in fitness in *Escherichia coli*.

Laboratory natural selection at different temperatures has been conducted previously on *Drosophila*. Lines of *Drosophila pseudoobscura* that were maintained at different temperatures for many years diverged significantly in size and in life history (Mourad 1965; Anderson 1966, 1973; Powell 1974). Similarly, lines of *D. melanogaster* maintained at different temperatures diverged in tolerance of extreme high temperature (Stephanou and Alahiotis 1983; Kilias and Alahiotis 1985; S. Cavicchi, personal communication), the stress-protein response (Stephanou et al. 1983), life history (Lints and Bourgois 1987), and body size and shape (Cavicchi et al. 1989, 1991). However, not all of these studies are replicated, and some of the results could be attributable to the effects of genetic drift.

Two conclusions emerge from these studies. First, thermal sensitivity of *Drosophila* can evolve very quickly, at least when the flies are *constrained* to be at a particular and constant temperature. Thus thermal sensitivity is heritable. Second, natural selection at nonextreme temperatures (e.g., 16.5° vs. 25°C) may have

correlated effects on performance and survival at extreme temperature. Thus a genetic correlation (albeit seemingly weak) exists between performance at intermediate temperature and tolerance of extreme temperature. Both findings are consistent with comparative data on lizards (above) and are relevant to speculations concerning the evolution of thermal sensitivity in response to pending climate change (Holt 1990; Hoffmann and Blows 1993; Parsons 1993).

Artificial Selection on Heat and Cold Tolerance

Does artificial selection for increased resistance to extreme heat lead to an evolutionary shift in heat resistance, and does it also lead to correlated shifts in other parts of the thermal performance curve (e.g., the optimal temperature, or in cold tolerance)? Answers to these questions would complement the above studies of laboratory natural selection.

The first evidence of heritable variation in resistance to extreme heat came from a study showing variation among isofemale lines of *D. melanogaster* (Hosgood and Parsons 1968). Artificial selection on tolerance of extreme heat or cold (or both) was first done by White et al. (1970) on a parasitic wasp (*Aphitis*). Observed responses to selection were positive, but the correlated responses were inconsistent (see Huey and Kingsolver 1989). Artificial selection on heat tolerance has also been conducted several times in *Drosophila,* originally on *D. melanogaster* by Morrison and Milkman (1978) and by Kilias and Alahiotis (1985), and also on *D. subobscura* by Quintana and Prevosti (1990). However, because *Drosophila* are usually weakened or sterilized by brief exposure to high temperature, the above three studies assayed the heat tolerance (percentage survival of an acute heat shock) of samples of flies drawn from isofemale lines. Then they selected for increased (or decreased) heat tolerance by using family selection (e.g., breeding from those isofemale lines with the highest heat tolerance). They all obtained direct responses to selection but did not examine possible correlated responses (e.g., in cold tolerance or in optimal temperature). Tucić (1979) selected on cold tolerance (percentage survival) at five different stages of development in *D. melanogaster.* The response was greatest in adults and least in larval and pupal stages. Selection for cold tolerance at one developmental stage affected cold tolerance at other stages, especially stages that were chronologically close to the one being selected.

We are repeating and extending those studies using an efficient new technique (Huey et al. 1992) that enables us to select directly on heat (or cold) resistance. We use an apparatus originally developed by Weber (1988) to measure resistance of flies to gas vapors. In brief, we add flies to a vertical glass column that has internal baffles and then raise the temperature of the column (and thus the flies) by heating water in a jacket surrounding the column. Eventually the flies become incapacitated by the heat and fall out of the column. By monitoring temperature within the column as flies fall out, we easily fractionate and score individual flies by their "knockdown" temperatures, which are analogous to the critical thermal maximum and minimum (temperatures at which righting responses are lost), widely used by vertebrate physiological ecologists as indexes of ecological death (Paladino et al. 1980). However, we can fractionate 1,000 flies by knockdown

temperature in about 25 min, a time during which we can score only one or two lizards.

To determine whether flies respond to artificial selection on knockdown temperature, we (Huey et al. 1992) conducted a pilot selection experiment. We ran single control and experimental lines through four generations of selection (top 25% of flies in each generation). (Because females mate randomly before selection, selection on males is random, such that the effective selection level is closer to 50%.) Selection was very successful and resulted in a mean increase in knockdown temperature of about 1.5°C for both males and females, which represents a shift of more than one phenotypic standard deviation in four generations.

We hope soon to extend this study to examine correlated shifts in the shape of the performance curve (e.g., shifts in cold tolerance, optimal temperature), as well as correlated effects on other resistance traits (Hoffmann and Parsons 1989, 1991), metabolic rate (Parsons 1993), and life-history traits (Service et al. 1985; Hoffmann and Parsons 1989; Parsons 1993). An understanding of such correlated shifts could be crucial to realistic predictions of evolutionary responses to climate change (Hoffmann and Blows 1993).

Artificial selection experiments on thermal sensitivity are at a formative stage in *Drosophila* and indeed with other ectotherms (White et al. 1970; Shah 1985). However, these experiments demonstrate that tolerance of extreme temperature responds to selection and that selection for performance at one temperature can sometimes cause correlated responses at some other temperatures (White et al. 1970; but see Lenski and Bennett 1993). Thus this line of research seems promising. Moreover, the conclusions drawn from selection experiments will be interesting to compare with those drawn from phylogenetic (comparative) studies of the evolution of thermal sensitivity in *Drosophila*.

EVOLUTION OF THERMAL PERFORMANCE AND CLIMATE CHANGE

The above section describes empirical studies showing how genetic constraints on the thermal performance curve may influence the evolutionary response to selection. However, these and other (Huey and Kingsolver 1989) experimental studies have all used either of two different approaches: truncation selection on tolerance of extreme heat or cold (see, e.g., White et al. 1970; Morrison and Milkman 1978) or a step change in the thermal environment (e.g., to some new, unchanging temperature; Stephanou and Alahiotis 1983; Lenski and Bennett 1993). These protocols are efficient but not especially realistic. How will thermal sensitivity evolve in response to more gradual changes in the thermal environment? This question is of practical importance, given the increases in global environmental temperatures expected during the next century (Schneider 1993). Theoretical models of evolution in temporally changing environments may help clarify some of the issues relevant to this question.

Recent studies by Lynch and colleagues (Lynch et al. 1991; Lynch and Lande 1993) consider the general problem of evolution of a quantitative trait in response to sustained, directional environment change. Their model considers a population with a single quantitative (polygenic) trait that experiences stabilizing selection

toward some optimal trait value. The population is initially in evolutionary equilibrium with respect to the environment, such that the mean trait value (Z) for the population matches the environmental optimum (Θ). The model then allows the environment to change gradually, such that the optimal trait value changes at a constant mean rate. Consequently, the mean trait value can begin to lag behind the environmental optimum. Lynch and Lande (1993) then ask two general questions of their model. First, how closely can the population track the environmental change? In other words, will the mean phenotype in the population stay close to the shifting optimal phenotype? Lynch and Lande (1993) show that for a sexual population of infinite size the steady-state lag is directly proportional to the rate of environmental change and inversely proportional to the genetic variance in Z and to the strength of stabilizing selection. Second, what is the maximum rate of environmental change that the population can tolerate without becoming extinct? Lynch and Lande (1993) show that this maximum rate of tolerable environmental change decreases with decreasing population size, decreasing genetic variation, and increasing environmental stochasticity.

Applying the Lynch and Lande Model to Thermal Sensitivity

With a few modifications, Lynch and Lande's (1993) general model can be reformulated to address two specific questions concerning the evolution of thermal sensitivity. First, does thermal performance breadth (fig. 1) affect the capacity of a population to track a sustained increase in environmental temperatures (i.e., climate change) and thus to avoid extinction? Second, do presumed tradeoffs between performance breadth and maximum performance (fig. 2*d;* jack-of-all-temperatures is a master of none; Huey and Hertz 1984; Lenski and Bennett 1993) affect these capacities?

The modified model is as follows. Consider a thermal performance curve (fig. 4) representing the performance R of an individual as a function of environmental (*not* body) temperature. (Performance here may represent developmental rate, reproductive rate, etc.) For simplicity, suppose the performance curve has the form of a normal function with a width (or breadth) characterized by σ_R (fig. 4). The maximum performance R_m for an individual occurs at some optimal environmental temperature Z. Suppose that all individuals have the same performance breadth σ_R but that they vary in their optimal temperature Z for performance, with phenotypic variance σ_Z^2 and genetic variance σ_g^2. Thus the population consists of individuals whose performance curves have identical shape but vary in position (i.e., in optimal temperature). Assume also that the fitness r (instantaneous rate of increase) of an individual is directly proportional to its performance, so that fitness $r = \alpha R$. Under these assumptions, stabilizing selection may be characterized as a normal function with width $\sigma_W = \alpha\sigma_R$. Finally, suppose that at time $t = 0$, the mean Z for the population is the same as the environmental temperature Θ. Thus the population is in evolutionary equilibrium. Then, as in Lynch and Lande (1993), the environmental temperature is increased over time at a constant rate k, which thus simulates climate warming.

This scenario can be readily related to Lynch and Lande's (1993) model, and indeed we can make direct use of some of their analytical results. We shall first

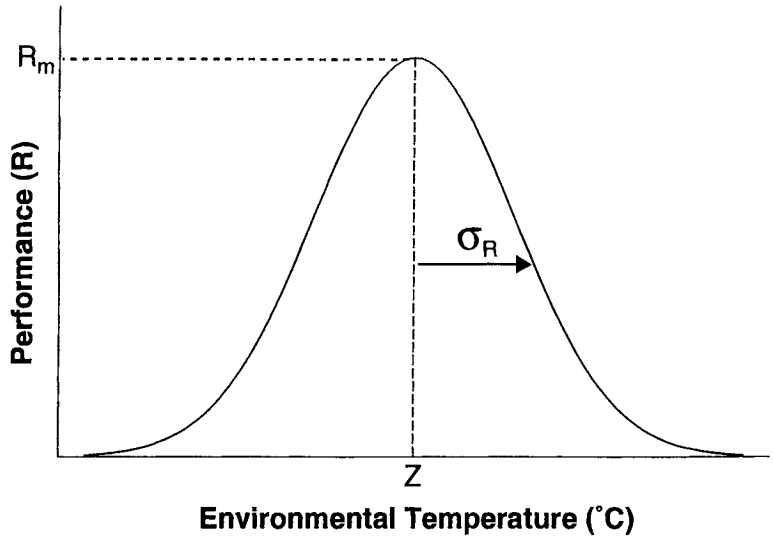

FIG. 4.—The effect of environmental temperature (in °C) on performance R of an ectotherm. Here performance is assumed to be a normal function characterized by a width σ_R and by a maximum value R_M occurring at the optimal temperature Z.

consider the case where the phenotypic and genetic variance in the population is independent of performance breadth (but see below). As environmental temperature increases, a lag λ (fig. 5) develops between environmental temperature Θ and the population mean phenotype $\bar{Z}$ (i.e., $\lambda = \Theta - \bar{Z}$). With time this lag approaches a steady-state value. From Lynch et al. (1991), one can show that, for an infinite sexual population with constant environmental change, this steady-state lag is

$$\lambda = \frac{k\alpha^2\sigma_R^2}{\sigma_g^2}. \tag{1}$$

As in the general case (Lynch and Lande 1993), the lag of the population behind the environmental optimum will be large if the rate of change of environmental temperature (k) is large but small if the genetic variance in optimal temperature is large. However, in the particular case in which performance breadth is allowed to vary, the lag will increase directly with the square of the thermal performance breadth (eq. [1]). Thus populations with large performance breadths will have limited capacity to track changes in the thermal environment (fig. 5).

Possibility of extinction.—Equation (1) suggests that populations with narrow thermal performance breadths will fare relatively well in the face of climatic change. However, this result ignores the possibility of population extinction. As Lynch and Lande (1993) have shown, as the rate of environmental change k increases, the lag of the mean population phenotype from the environmental optimum increases until the mean absolute fitness $\bar{r}$ in the population approaches zero; when $\bar{r} < 0$, the population, of course, becomes extinct. Lynch and Lande

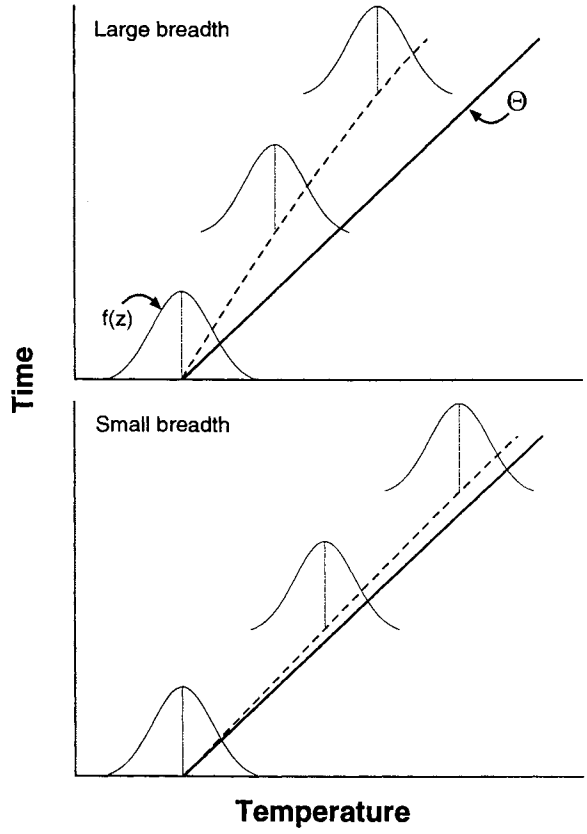

FIG. 5.—Diagram illustrating the effect of thermal performance breadth (fig. 1) on a population's evolutionary response to climate warming. Here $f(Z)$ is the frequency distribution of phenotypic trait Z, the optimal temperature for performance. In each panel, the *solid line* represents the change in environmental temperature (Θ), and the *dashed line* represents the change in the population mean value of Z with time. As time proceeds, a lag develops between the environmental optimum and the population mean phenotype. For populations with large thermal performance breadths (*upper panel*), this lag will be greater than for populations with small performance breadths (*lower panel;* see eq. [1]).

(1993) show that there is a critical rate of environmental change k_c above which population extinction will necessarily occur. For an infinite population, this critical rate of climate change for our problem (above) is

$$k_c = \frac{h^2\sigma_Z^2}{\alpha\sigma_R}\left(2\alpha R_m - \frac{\sigma_Z^2}{\alpha^2\sigma_R^2}\right)^{0.5}, \qquad (2)$$

where h^2 is the heritability σ_g^2/σ_Z^2.

Of particular interest here is the dependence of k_c on the thermal performance breadth. Taking appropriate derivatives, one can show that an intermediate value of performance breadth σ_R maximizes the value of k_c (and thus maximizes the

rate of tolerable environmental change); this value occurs when

$$\frac{\sigma_R}{\sigma_Z} = (\alpha^3 R_m)^{-0.5}. \quad (3)$$

Note that, for our problem, both σ_R and σ_Z have units of temperature (°C); thus σ_R/σ_Z represents the thermal performance breadth relative to the standard deviation for phenotypic variation in optimal performance temperature in the population. The reason for this dependence of k_c on thermal performance breadth is as follows: For large performance breadths, the lag of the population mean behind the environmental optimum is large, so that most of the population will have low fitness values, and the population becomes extinct more readily. For narrow performance breadths, the lag is small, but performance (and thus fitness) falls off rapidly with departures from the optimum, so that most of the population will again have low fitness. In fact, there is a minimum performance breadth below which the mean population fitness is zero even in the absence of environmental change (i.e., $k_c = 0$); this minimum occurs when

$$\frac{\sigma_R}{\sigma_Z} = (2\alpha^3 R_m)^{-0.5}. \quad (4)$$

Thus intermediate performance breadths will allow the population to maximize rates of evolutionary change and to reduce the incidence of extinction at higher rates of environmental change. Note that this "optimal" performance breadth will be small when the maximum performance R_m is greater.

Figure 6 shows a representative plot of k_c as a function of σ_R (*solid line;* parameter values specified in the figure legend). Note that k_c has units here of °C/generation. As σ_R increases, k_c increases rapidly to a maximum, then declines slowly toward zero. For the parameter values in figure 6, the maximum tolerable rate of climate change without extinction is 0.5°C/generation. Thus for organisms with generation times on the order of 1 decade, performance breadths may have a crucial impact on whether a population evolves or goes extinct in response to the projected rates of climate warming expected during the next century (Schneider 1993). These calculations are based on an effectively infinite population size and a deterministic environmental change: Lynch and Lande (1993) show that, for small population sizes and stochastic environments, the values for k_c will be decreased substantially. Nevertheless, our qualitative conclusions remain unchanged (see below).

Role of trade-offs.—The above considerations assume that performance breadth σ_R and maximum performance R_m vary independently of each other. However, trade-offs may exist between performance breadth and maximum performance (fig. 2*d;* but see Lenski and Bennett 1993). How would such trade-offs affect our conclusions about performance breadth and the evolutionary response to climate change? Two results are of interest. First, the lag of mean population phenotype from the environmental optimum is *not* affected by such trade-offs, as shown by equation (1). Second, trade-offs between breadth and maximum performance will tend to decrease the performance breadth at which k_c is maximum. For example, consider a trade-off such that R_m is inversely proportional to

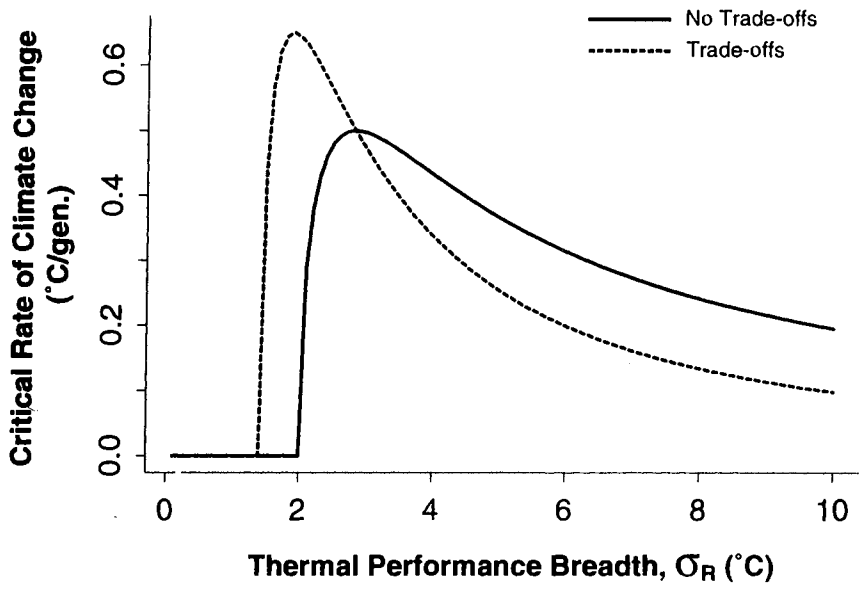

FIG. 6.—Theoretical predictions of the critical rate of climate change (k_c, in °C/generation) above which population extinction will occur, as a function of thermal performance breadth σ_R (in °C). Parameter values for these simulations are $\sigma_Z^2 = 4°C^2$, $\alpha = 1$, and $h^2 = 0.5$. The *solid line* indicates the case in which no trade-off exists between maximum performance (R_m) and performance breadth (σ_R) of an individual. In this case $R_m = 0.5$/generation is the maximum instantaneous rate of increase. The *dashed line* indicates the case in which a trade-off does exist between maximum performance and performance breadth, such that the product of R_m and σ_R equals a constant value ($C = 1.414$). See text for further explanation.

σ_R (i.e., $R_m\sigma_R = C$, a constant). By substituting into equation (2) and by taking derivatives, one can show that an intermediate value of performance breadth σ_R still yields the maximum value of k_c; this value now occurs when

$$\frac{\sigma_R}{\sigma_Z} = \frac{2\sigma_Z}{3\alpha^3 C}. \tag{5}$$

The minimum performance breadth below which the mean population fitness is zero even in the absence of environmental change (i.e., $k_c = 0$) now occurs when

$$\frac{\sigma_R}{\sigma_Z} = \frac{\sigma_Z}{2\alpha^3 C}. \tag{6}$$

Such a trade-off between maximum performance and performance breadth generally decreases the value of σ_R at which k_c is maximum (*dashed line* in fig. 6). In addition, relative to the case in which no trade-offs exist, the trade-off leads to larger absolute values of k_c when performance breadths are narrow and smaller values of k_c when breadths are wide (fig. 6). Thus trade-offs between breadth and maximum performance will further favor populations in which individuals have narrow thermal performance breadths.

These effects of performance breadth on the ability of populations to track

climate change result from the direct relationship between performance breadth and the intensity of stabilizing selection. Larger performance breadths mean that the fitness consequences of nonoptimal phenotypes are relatively smaller, so that the strength of stabilizing selection is relatively weaker. As discussed by Lynch and Lande (1993), as the strength of stabilizing selection decreases, the evolutionary response to selection also decreases, so the lag of the population from the environmental optimum increases, until extinction occurs.

Genetic variation and performance breadth.—The above analyses assume that the genetic and phenotypic variance (and thus the heritability) of optimal temperature in the population is independent of performance breadth. However, theoretical reasons suggest that this assumption may not be valid in some cases. To see this possibility, recall that the genetic variance in a trait reflects a balance of mutation, drift, and selection. In small populations in which drift prevails over selection, the equilibrium genetic variance is primarily the result of a mutation-drift balance (see, e.g., Lynch and Hill 1986) and thus will be independent of performance breadth. However, as population size and the strength of selection increase, selection will increasingly influence the genetic variance as well as performance breadth. How will this affect our earlier conclusions? To address this question, we will use Lynch and Lande's (1993) result for the equilibrium genetic variance for an infinite sexual population, based on Kimura's (1965) "infinite-alleles" model. Note however that alternative models (e.g., Turelli's [1984] "house-of-cards") give somewhat different predictions for the genetic variance (see below).

Lynch and Lande (1993) show that the equilibrium genetic variance for a quantitative trait undergoing stabilizing selection and mutation in an infinite sexual population is given by

$$\sigma_g^2 = \sigma_W \sigma_m (2n_e)^{0.5}, \tag{7}$$

where σ_m is the rate of input of new genetic variation due to mutation and n_e is the effective number of segregating factors. Because $\sigma_W = \alpha\sigma_R$, the genetic variance in the population will be directly proportional to the performance breadth. Recalling that the phenotypic variance is simply the sum of the genetic variance plus the environmental variance σ_E^2, we can substitute these relations into our analyses of evolutionary responses to climate change. Several interesting results emerge. First, the steady-state lag of the population from the environmental optimum as climate changes now becomes

$$\lambda = kM\alpha\sigma_R, \tag{8}$$

where $M = \sigma_m(2n_e)^{0.5}$. Comparing this result to equation (1), we see that the lag is now less dependent on performance breadth. Second, we can readily solve for the critical rate of climate change k_c, above which a population becomes extinct; this rate occurs when

$$k_c = M\left(2\alpha R_m - \frac{\sigma_E^2}{\alpha^2\sigma_R^2} - \frac{M}{\alpha\sigma_R}\right)^{0.5}. \tag{9}$$

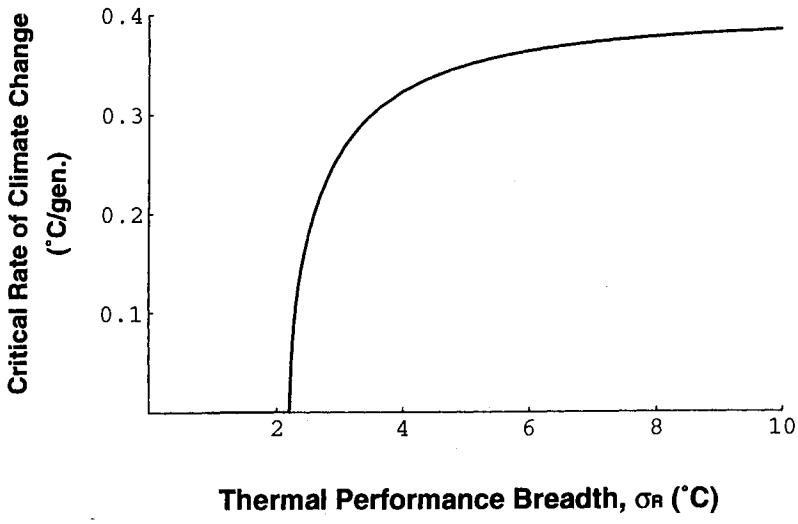

FIG. 7.—Theoretical predictions of the critical rate of climate change (k_c, in °C/generation) above which population extinction will occur, as a function of thermal performance breadth σ_R (in °C), where genetic variance depends on performance breadth (eq. [7]). Parameter values for this simulation are $\sigma_E^2 = 4°C^2$, $\alpha = 1$, $R_m = 0.5$/generation, and $M = \sigma_m(2n_e)^{0.5} = 0.4$. See text for further explanation.

One can readily show that no positive, finite value of σ_R maximizes k_c. Inspection of equation (9) shows that, as performance breadth increases to infinity, the critical rate of climate change asymptotically approaches $M(2\alpha R_m)^{-0.5}$. Numerical calculations (fig. 7) suggest that k_c approaches this asymptotic value rather quickly as performance breadth increases: thus, above some minimum value of performance breadth, the critical rate of climate change is relatively independent of performance breadth. This observation is in sharp contrast to our previous results, which assumed a constant heritability, where k_c is maximized at rather small values of performance breadth (fig. 6). Interestingly, if we incorporate a trade-off between maximum performance and performance breadth as described above, this does not change the qualitative outcome: k_c still increases to some asymptotic value as performance breadth increases. However, this may depend on the particular trade-off under consideration.

Thus, allowing the genetic variance and heritability to increase with increasing performance breadth qualitatively changes our predictions about the consequences of performance breadth for the evolutionary response to climate change. However, no general consensus exists among theoreticians as to the most appropriate way to model the genetic variance in a population under a balance of mutation, drift, and stabilizing selection (Lande 1975; Turelli 1984; Barton and Turelli 1989), but in smaller populations the effects of selection (and hence performance breadth) on the genetic variance will likely be smaller. Hence we are left with the empirical question: Do the genetic variance and heritability of optimal performance temperatures in natural populations vary systematically with performance breadth? We know of no data that address this question; our analyses

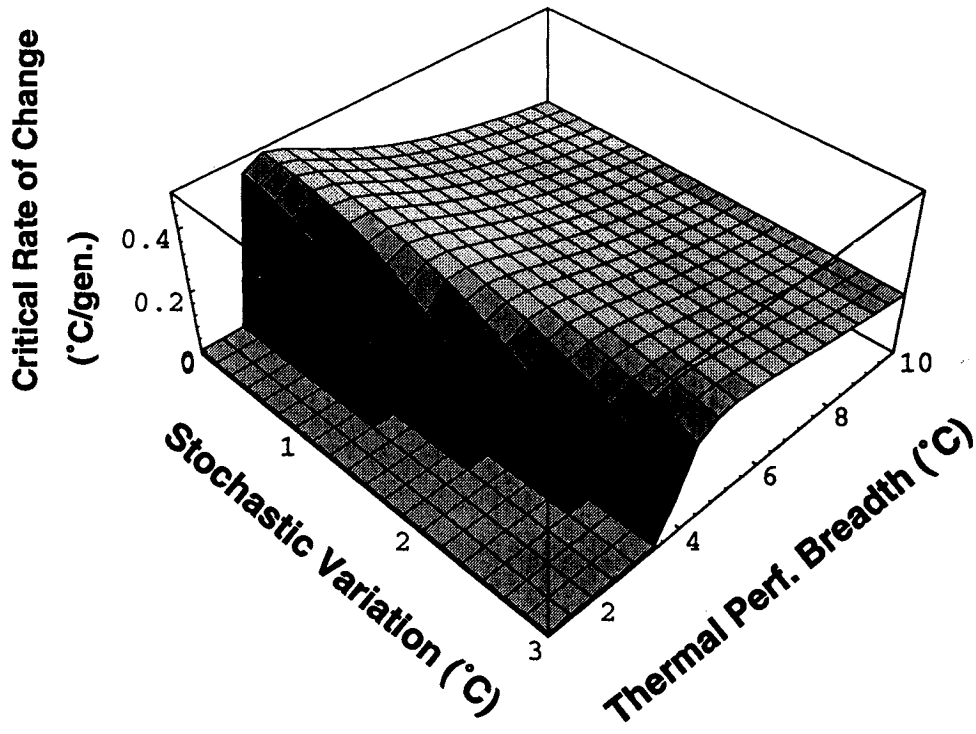

FIG. 8.—Theoretical predictions of the critical rate of climate change (k_c, in °C/generation) above which population extinction will occur, as a function of thermal performance breadth σ_R (in °C) and the amount of stochastic climatic variation σ_θ (in °C). Parameter values for these simulations are identical to those in fig. 6 for the case in which no trade-off exists between maximum performance and performance breadth. See text for further explanation.

suggest that the answer is crucial to predicting the evolutionary outcome of climate change.

Stochastic climatic variation and performance breadth.—The models considered thus far incorporate only deterministic environmental changes. The consequences of adding stochastic environmental variation to the model are also instructive. Following Lynch and Lande (1993), let the expected value of the environment change linearly over time, but now with stochastic variation with mean zero and standard deviation σ_θ distributed normally about this directional trend. For our case of directional climate change (with constant h^2 and without trade-offs between breadth and maximum performance), adding such stochastic climatic variation has several interesting effects on the relationship between thermal performance breadth and the critical rate of climate change, k_c (fig. 8). First, the qualitative dependence of k_c on performance breadth is not changed by stochastic variation: there is an intermediate performance breadth yielding the maximum critical rate of climate change. Second, increasing stochastic variation increases the performance breadth at which k_c is maximized: stochastic variation favors broader performance breadths. Third, increasing stochastic variation de-

creases the critical rate of climate change, regardless of performance breadth. Finally, increasing stochastic variation decreases the sensitivity of k_c on performance breadth. Thus, the model predicts that increasing stochastic variation in climate will favor larger performance breadths, but an intermediate performance breadth still maximizes the critical rate of climate change even in the absence of trade-offs, and such stochastic variation will increase the likelihood of extinction (Lynch and Lande 1993).

Summary

In summary, we have applied models developed by Lynch and colleagues to address the question, How do the shapes of thermal performance curves influence the evolutionary responses of a population to directional climate change? We have considered the specific case in which genetic and phenotypic variation exists in the optimal temperature for fitness-related performance, and we have examined the capacity of the population both to track (evolutionarily) climate change and to avoid extinction. Our analyses are primarily for infinite populations with deterministic environments, but many of the qualitative conclusions are the same for finite populations and for stochastic environments (see fig. 8; Lynch and Lande 1993).

Our analyses yield several main results. The lag of the mean phenotype (the mean optimal performance temperature) in the population behind the environmental temperature depends on the rate of climate change and on the performance breadth. Thus, increased rates of climate change as well as increased performance breadths decrease the evolutionary capacity of the population to track climate change. Our other results depend crucially on the possible relationship between the genetic variation in optimal temperature and the performance breadth. If genetic variation (and heritability) is independent of breadth, then an intermediate value of performance breadth allows the population to sustain evolutionary change (and to avoid extinction) at the highest rates of climate change: either lower or higher values of performance breadth increase the likelihood of extinction in the face of climate change. In this case, the existence of trade-offs between thermal performance breadth and maximum performance will decrease the performance breadth at which the maximum rate of sustainable environmental change occurs. On the other hand, if genetic variation increases with increasing breadth, then the maximum sustainable rate of climate change for a population increases with increasing performance breadth, quickly reaching a maximum asymptotic value. These results clearly demonstrate the central importance of thermal performance curves and of genetic and phenotypic variation in thermal performance for predicting possible evolutionary responses to climate change.

CONCLUDING REMARKS

The article has presented three very different views of the evolution of thermal sensitivity. In concluding we wish to reemphasize the benefits of looking at evolutionary issues from several complementary perspectives.

Phylogenetic studies such as those presented above for iguanid lizards effec-

tively elucidate long-term patterns of evolutionary change within a clade (Harvey and Pagel 1991). In effect, such studies reveal the patterns of evolution that have actually occurred in nature. As such, they are extremely valuable. Indeed, in the absence of fossil indicators of traits of extinct organisms, comparative studies provide our only access to the history of trait evolution. However, powerful as they are, comparative approaches suffer from several philosophical limitations (Huey and Bennett 1986) and do not provide a complete view of the evolutionary process. For example, it remains to be shown whether historical patterns serve as reliable guides of how contemporary populations will respond to selection in the future. Even so, comparative patterns can suggest hypotheses concerning future evolution. For example, we used comparative data on lizards to hypothesize a genetic correlation between an ectotherm's optimal temperature and its critical thermal maximum. The limited data currently available from selection experiments with flies appears consistent with that hypothesis.

Laboratory selection experiments are an alternative approach designed to illuminate the short-term dynamics of evolutionary processes (Clark 1987; Stearns 1989; Rose et al. 1990). They directly establish realized heritabilities, validate genetic correlations, and generate lines suitable for genetic and mechanistic studies (Graves et al. 1992). Moreover, the results of selection experiments should be relevant to rapid global change (Hoffmann and Blows 1993). Yet selection experiments are, of course, highly artificial, for typically only one variable is manipulated at a time, and the selection protocols themselves are usually unnatural (Rose et al. 1990).

Mathematical models of evolution within populations can help us to identify key aspects of the problem and sometimes to make nonintuitive predictions about the outcome of evolution. In the present case our application of Lynch and Lande's (1993) model to the evolutionary response to progressive climate change highlights an essential relationship between thermal performance breadth and the strength of stabilizing selection. Moreover, it makes the somewhat surprising prediction that whether populations with narrower or broader performance breadths will generally fare better evolutionarily in the face of rapid climate change depends critically on assumptions about the determinants of genetic variation in performance. Such theoretical predictions can help to direct or provoke relevant empirical studies of the evolutionary and genetic consequences of performance breadth and performance trade-offs (Lenski and Bennett 1993).

Thus these different approaches presented here are fully complementary: they reciprocally illuminate different aspects (and time scales) of the evolutionary process. Of course, these three approaches are not the only perspectives relevant to an understanding of evolution, and additional types of studies will be necessary for a more complete analysis. For example, field studies are required to elucidate the patterns and intensity of natural selection on thermal sensitivity in contemporary populations (see, e.g., Holland et al. 1974; Christian and Tracy 1981). Moreover, direct studies of the mechanistic physiology will be required to understand evolutionary shifts that underlie performance curves. Given the renewed relevance of studies of the evolution of thermal sensitivity (Hoffmann and Blows 1993), considerable progress can be expected soon on all of these different approaches.

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