Temperature, Demography, and Ectotherm Fitness

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Temperature has profound effects on ectotherms such as plants, invertebrates, and lower vertebrates (Hochachka and Somero 1984; Cossins and Bowler 1987). The impact of temperature is often depicted graphically as a "thermal performance curve," which plots performance as a function of body temperature (Huey and Stevenson 1979). Typically, performance increases gradually with temperature up to some maximal or optimal level but then declines precipitously as temperature approaches damaging levels and upper lethal limits.

The impact of temperature on Darwinian fitness of ectotherms can be depicted similarly. However, one must first choose an appropriate measure of fitness (Stearns 1982). Several measures are available (Tuljupurkar 1990; Roff 1992; Stearns 1992; Carey 1993; Kozlowski 1993; Charlesworth 1994), but r ("intrinsic rate of increase"; see "Material and Methods") and R_o ("net reproductive rate"; see "Material and Methods") are by far the two most commonly used ones. The intrinsic rate of increase is the rate of population increase in a closed population, assuming constant age-specific schedules of death and reproduction and a stable age distribution, whereas the net reproductive rate is the average number of female offspring born to a female over her lifetime, again assuming constant age-specific schedules of death and reproduction (Carey 1993). Both measures estimate population growth rates, but r is scaled to time, whereas R_o is scaled per generation and is independent of time. Surprisingly, however, whether these alternative fitness measures have parallel responses to temperature has not previously been addressed systematically. Should r and R_o actually have different temperature sensitivities, then biologists attempting to predict how populations will respond to climate change (e.g., Dunham 1993; Huey and Kingsolver 1993; Lynch and Lande 1993; Wennergren and Landin 1993) will need to select between these alternative fitness measures with special care (Travis and Henrich 1986).

To evaluate whether r and R_o show similar thermal sensitivities, we took an empirical approach and searched the demographic literature for studies in which both fitness measures were quantified at three or more temperatures. Prior to making that search, however, we predicted that thermal fitness curves for the two fitness measures would in fact be different, such that the fitness curve for r should be biased toward higher temperatures (thus, "right shifted") relative to that for R_o. We arrived at this prediction by linking two well-established observations. First, generation time (T) is generally inversely related to temperature in ectotherms (Taylor 1981). Second, r is inversely and strongly related to generation time, whereas R_o is independent of generation time (Cole 1954; Lewontin 1965). Consequently, the shortening of generation time by high temperatures will in effect increase r but will not affect R_o, thus leading to a right-shifted thermal fitness curve for r. Of course, high temperatures will also shorten life span (Pearl 1928; Shaw and Bercaw 1962) and potentially lower fecundity, but these effects rarely offset the dominant impact of a shortened generation time (Cole 1954; Lewontin 1965).

Our prediction of a right-shifted fitness curve for r relative to that for R_o is admittedly obvious from a joint consideration of thermal physiology and demography, but that prediction becomes obvious only after one asks whether thermal fitness curves for r and R_o should be congruent. To our knowledge, however, that question has previously been asked only in passing (Ricci 1991) despite scores of articles that have tabulated relevant demography data or that have speculated on the effect of temperature on population dynamics (see below). Seemingly obvious questions are not always asked, and even obvious predictions still require testing (Travis and Henrich 1986).

The data set we compiled also enables us to examine

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Table 1: Thermal sensitivity of fitness (for r and R_o) for various taxa of ectotherms

Taxon	n species	Mean thermal center of mass: For r	For R_o	Average difference	% with $T_{r\text{-}max} > T_{Ro\text{-}max}$
Ascomycetes	1	24.9	23.0	1.76	100
Rotifera	4	20.2 ± .97	18.3 ± 2.47	1.85 ± .761	75
Nematoda	2	20.4 ± 1.96	18.5 ± 1.98	1.93 ± .001	50
Gastropoda	2	25.5 ± 6.93	25.0 ± 9.94	.44 ± .271	50
Polychaeta	1	23.9	23.5	.38	100
Crustacea	7	20.4 ± 5.20	18.2 ± 5.90	2.21 ± .129	71
Acarina	9	27.1 ± .048	25.9 ± .81	1.18 ± .358	67
Thysanoptera	3	26.9 ± 1.48	25.7 ± 1.74	1.26 ± .709	33
Hemiptera	2	28.9 ± 3.01	27.1 ± .14	1.77 ± 1.837	100
Homoptera	21	22.6 ± 2.78	20.3 ± 3.42	2.30 ± .286	86
Coleoptera	6	28.7 ± 3.40	27.3 ± 5.52	1.34 ± .511	67
Lepidoptera	5	26.8 ± 1.74	26.1 ± 2.48	.73 ± .147	60
Diptera	8	26.0 ± .77	24.7 ± .48	1.26 ± .311	75
Hymenoptera	7	26.8 ± 4.20	24.9 ± 2.77	1.93 ± .342	100
Total	78	24.6 ± .43	23.0 ± .48	1.68 ± .135	75.6

Note: $T_{r\text{-}max}$ and $T_{Ro\text{-}max}$ are the optimal temperatures for r and R_o, respectively. Mean thermal center of mass is defined in "Material and Methods." Units are in °C ± SE.

how well the thermal dependence of two commonly used proxies for fitness (development time and lifetime fecundity) correlate with the thermal dependence of fitness itself. Evolutionary biologists have long known that development time generally has a much larger impact on r than does lifetime fecundity, at least when analyses are conducted on life-table data gathered at a single temperature (Cole 1954; Lewontin 1965; Travis and Henrich 1986; Stearns and Kawecki 1994). However, does this same pattern hold when comparisons are made across temperatures? If so, then estimates of the thermal sensitivity of development time might be a more reliable index of the thermal sensitivity of fitness than is lifetime fecundity, at least when r is the appropriate fitness measure (Kozlowski 1993).

Material and Methods

We searched for studies with life-table data gathered at three or more constant temperatures ($\overline{X} = 4.7$, range three to eight). We then extracted estimates of r and R_o at each test temperature. Where possible, we also extracted estimates (see Carey 1993) of generation time (T), development time from egg to adult (T_{ea}), development time from egg to egg (T_{ee}), and lifetime fecundity (M_x). Not surprisingly, quite diverse methods have been used to calculate these parameters. Most studies (at least 62%) in our sample estimated r via the classical Lotka equation (Carey 1993; Charlesworth 1994), a few (7%) used the analytical approximation $r = \ln R_o/T$ (see Carey 1993), and the remainder (31%) were vague about methods.

We made no attempt to search exhaustively, but we nevertheless found numerous examples from diverse taxa and lifestyles. Not surprisingly, the vast majority are Arthropoda (table 1), but a number of other taxa are represented, including a fungus (Ascomycota) and two worms (Nematoda). Although this data set is phylogenetically diverse, it is hardly ideal for comparative analyses. For one thing, it is heavily biased toward economically important arthropods (especially insects and mites). Moreover, many important taxa are unrepresented; remarkably, we were unable to find data for any higher plant or for any vertebrate ectotherm. Some species are represented by multiple geographic strains, different genotypes or experimental treatments, or by separate studies of the same species. To reduce pseudoreplication, we analyzed only a single sample per species, leaving 78 included species. We used sequential criteria for choosing (e.g., the study with the most temperature levels or the most recent). (Note that among the data sets excluded by these criteria were two [*Macrotrachela quadricornifera* "c," Ricci 1991; *Biomphalaria pfeifferi*, Schiff and Garnett 1967] in which the weighted mean temperature of r was lower than that of R_o, contrary to the pattern found in almost all other species [see below] and in other samples of these species.) The species, fitness data, and associated citations are available from the authors on request and in the online edition of the *American Naturalist.*

We compared the temperature sensitivity of r and R_o in two different ways. First, to detect differences in general position for the whole fitness curves, we computed a "thermal center of mass" for both r and R_o (within species):

each test temperature was weighted by the observed value of fitness measure and then averaged across temperature. Thus, if the curve for r is right shifted relative to that for R_o, then the thermal center of mass for r will be at a higher temperature than that for R_o. Second, we also determined whether the "optimal test temperature" (i.e., the specific experimental temperature at which a given fitness measure was maximal) for r was higher than that for R_o. Note that temperature intervals in most of these studies are broad ($\overline{X} = 3.9$°C intervals), such that subtle differences in optimal temperatures will often be missed (Type II error).

To determine whether observed differences (see below) in the thermal sensitivity of r versus R_o mainly result from the effects of temperature on generation time (T), we "corrected" thermal sensitivities of r for generation time (T). For each species at each temperature, we multiplied r by T/T_{max} and then recalculated the thermal center of mass; this procedure transforms estimates of r onto a physiological time scale (Taylor 1981). If this correction eliminates differences in the thermal sensitivities of r and R_o, we can attribute the uncorrected differences to the influence of temperature on generation time.

To determine which of two correlates of fitness (development time vs. lifetime fecundity) better predicts Darwinian fitness (r), we calculated correlation coefficients for r with development time (or generation time if development time was unreported) and for r with lifetime fecundity (studies with more than three temperatures). We then used a Wilcoxon rank-sum test to compare magnitude of the two correlations, paired within species. We also tabulated the proportion of cases in which the optimal temperature for r coincided with that for lifetime fecundity and that for development time.

Results

Thermal Sensitivity of r *versus* R_o

We show representative plots of r and R_o (each normalized to their maximum value) versus temperature for several phylogenetically diverse ectotherms (fig. 1). In these examples, the optimal temperature for r ($T_{r\text{-}max}$) is generally higher than that for R_o ($T_{Ro\text{-}max}$), and the curves for r are invariably right shifted relative to those for R_o.

Next, we tested our prediction that the fitness curve for r would be shifted to higher temperatures than that for R_o. Indeed, the thermal center of mass for r was higher (that is warmer) than that for R_o in 77 of 78 species (table 1). The one exceptional species is a lepidopteran, *Chilo partellus* (Singh 1991). We cannot tell whether this anomalous study is valid or whether it instead represents a calculation or printing error. In any case, this pattern is essentially universal.

The experimental temperature at which r was maximal ($T_{r\text{-}max}$) was higher than that for R_o ($T_{Ro\text{-}max}$) in 71.8% of the samples (table 1). In all remaining cases (except *C. partellus*, above), $T_{r\text{-}max}$ and $T_{Ro\text{-}max}$ were the same.

As noted above, we expected that the fitness curves for r versus R_o would differ primarily because of the effect of temperature on generation time. We tested this assumption by transforming the fitness data for r onto a "physiological time scale" (Taylor 1981) and then recalculated the thermal center of mass for r. The mean difference ($\pm$ SE) between thermal centers of mass for r versus R_o prior to transformation was 1.7° $\pm$ 0.16°C but only 0.33° $\pm$ 0.19°C ($n = 62$) after transformation. If we delete two outliers (for *Eurytemora hirundoides* and *Gammarus lawrencianus*), the after-transformation estimate is even closer to zero (0.13° $\pm$ 0.11°C). Thus, transforming the fitness data onto a physiological time scale eliminates, on average, the differences in thermal center of mass between r and R_o. (Note that this pattern holds if fitness data are corrected with either of two estimates of development time [egg to adult or egg to egg] rather than with generation time [results not shown].)

Correlates of Fitness

Biologists often need information on the effects of temperature on fitness. However, many will find it impractical to generate full life tables at multiple temperatures, and such workers will need to substitute a proxy for fitness. Which proxy for fitness—development time or lifetime fecundity—is the better predictor of fitness at different temperatures? The answer depends in part, of course, on whether r or R_o is the better fitness index, although r seems to be applicable to more diverse demographic scenarios than R_o (Roff 1992; Stearns 1992; Kozlowski 1993). Interestingly, development time (egg to adult) was in fact a much stronger predictor of r across temperatures (fig. 2; $\overline{X} = 0.684 \pm 0.0541$, $n = 53$) than was lifetime fecundity (fig. 2; $\overline{X} = 0.456 \pm 0.0689$, $n = 53$). The significance of this difference was underscored in a paired test ($P = .01$).

This same issue can also be approached by determining whether the temperature that maximizes r is closer to the temperature that maximizes R_o or to that minimizing development time. As noted above, the temperature optimum for r was significantly less likely (χ^2 test, $P = .01$) to coincide with that for R_o (27.3% of species sampled) than was that for development time (egg to adult, 50.1%). Moreover, the temperature optimum for r averaged substantially farther from that for R_o (4.9° $\pm$ 0.47°C) than from that for development time (−2.2° $\pm$ 0.30°C).

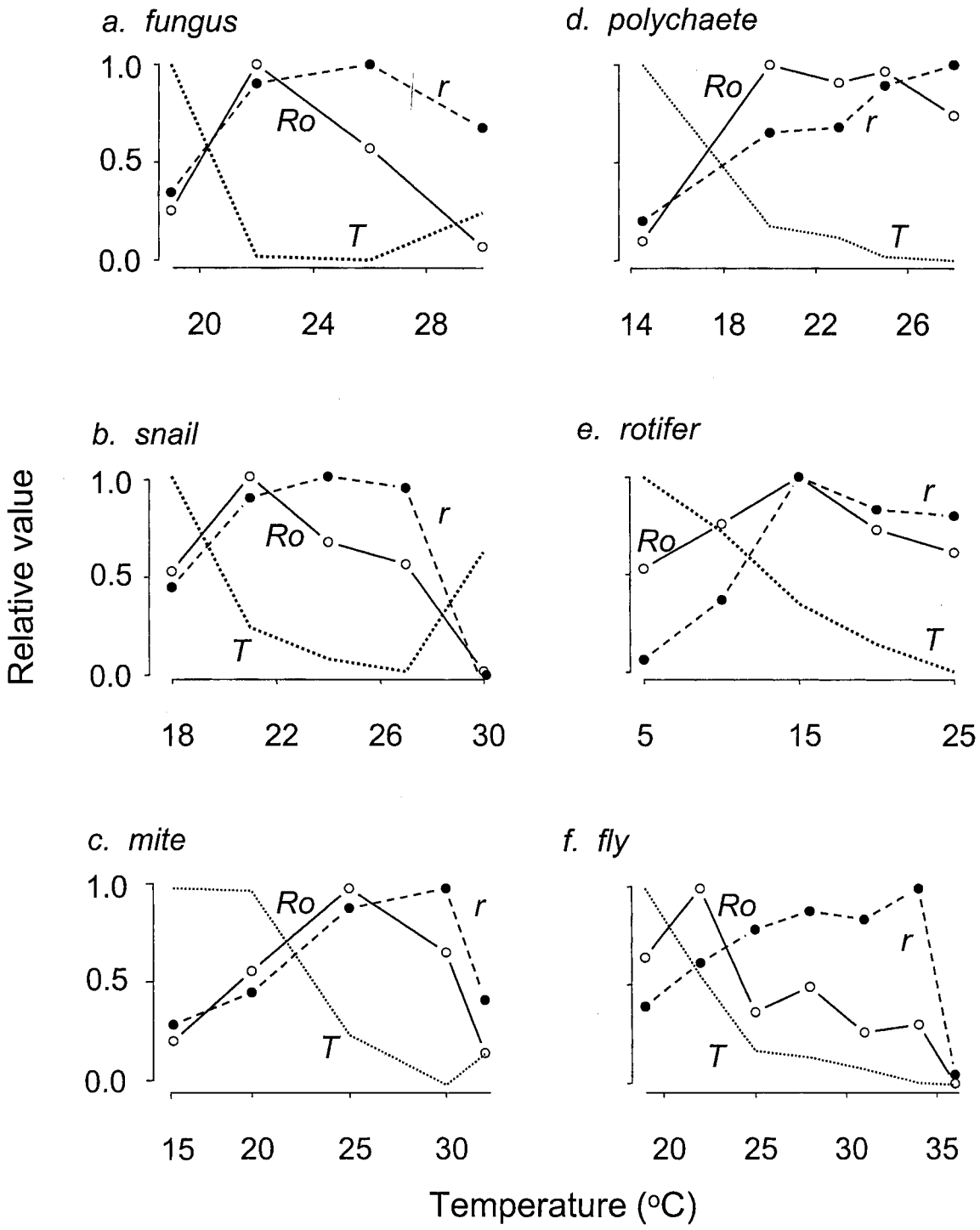

Figure 1: Effect of temperature on two fitness measures (r and R_o) and on generation time (T) for diverse ectotherms: (*a*) *fungus* (*Uncinula necator*; Chellemi and Marois 1992), (*b*) *snail* (*Biomphalaria pfeifferi*; de Kock and Joubert 1991), (*c*) *mite* (*Galendromus helveolus*; Caceres and Childers 1991), (*d*) *polychaete* (*Ophryotrocha labronica*; Åkesson 1976), (*e*) *rotifer* (*Keratella cochlearis*; Walz 1983), and (*f*) *fly* (*Bactrocera dorsalis*; Yang et al. 1994).

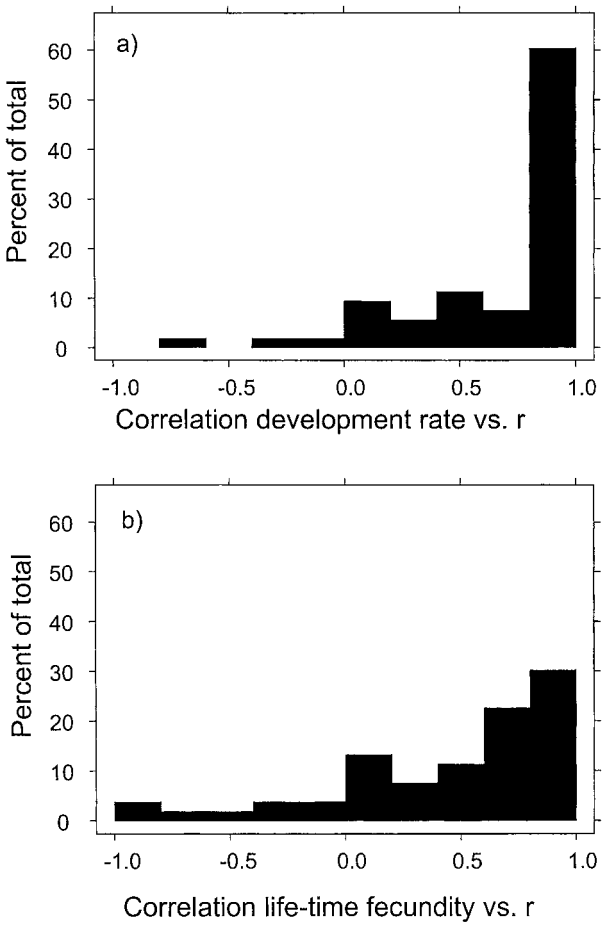

Figure 2: Histograms of Spearman rank correlation coefficients (*a*) for development rate (1/development time) versus *r* and (*b*) for lifetime fecundity (M_x) versus *r*. Development rate is a more reliable predictor of *r* across temperature than is lifetime fecundity (but see "Discussion"). (Note that the same pattern holds if development time rather than development rate is used, although the correlation coefficients have reversed signs.)

Discussion

Two classical measures of fitness, *r* and R_o, are widely used in evolutionary ecology. The philosophical and mathematical differences between these measures are well understood in principle (Caswell 1989; Roff 1992; Stearns 1992; Kozlowski 1993; Charlesworth 1994), but their differences in thermal sensitivity have not been compared systematically. We show that these two measures in fact have strikingly different thermal sensitivities; specifically, temperatures that maximize *r* are usually higher than those that maximize R_o (fig. 1; table 1). This result is essentially universal and holds in seven phyla of ectotherms.

The observed differences in the thermal sensitivity of *r* and R_o validate our predictions (see the introduction to this note). Those predictions follow from the recognition that high temperatures will shorten generation time (fig. 1; Pearl 1928), which in turn will inflate *r* at high temperature but will not impact R_o. Indeed, when we factored out the impact of temperature on generation time, differences in thermal sensitivity of *r* versus R_o were essentially eliminated.

Evolutionary ecologists (Travis and Henrich 1986; Roff 1992; Stearns 1992; Kawecki and Stearns 1993; Kozlowski 1993; Berrigan and Koella 1994; Charlesworth 1994) have warned that classical fitness measures (*r* and R_o) are not interchangeable and, consequently, that choice between measures must be guided by basic demographic context of the population at hand (e.g., whether the population is stable or has overlapping generations). Complicating matters further is the possibility that the appropriate fitness measure may change seasonally even for a given population (Bradshaw et al. 1998). Our discovery that *r* and R_o can differ strikingly in their sensitivity to temperature adds an important physiological reinforcement of that demographic warning. Consider, for instance, a population for which *r* is the demographically correct fitness measure: data on the thermal dependence of R_o (fig. 1) or on lifetime fecundity (fig. 2*b*) will likely lead to incorrect predictions of how the population will respond to climate change or to habitat shift (see Dunham 1993; Huey and Kingsolver 1993; Lynch and Lande 1993). Similarly, using inappropriate data might also encourage applied biologists to choose nonoptimal thermal regimes for rearing organisms for release as biocontrol agents (Yang et al. 1994; Scott et al. 1997). Recall that the optimal temperature for *r* averages 4.9°C higher than that for R_o.

For many biologists, the choice between *r* versus R_o is, of course, academic, as few will have access to (or find it practical to generate) life-table data gathered at multiple temperatures. Even so, they may still need to know how temperature affects the fitness of their target species. In the absence of life-table data, many biologists (ourselves included) have used development time or fecundity as a proxy for fitness. Fortunately, our analysis confirms that both traits are usually positively correlated with *r* across temperature, but development time was a much stronger predictor of *r* than was lifetime fecundity. Moreover, measuring the thermal dependence of development time will generally be easier (or at least faster) than measuring the thermal dependence of lifetime fecundity. Nevertheless, the thermal development time is far from a perfect predictor of *r*: the optimal temperatures of these two measures coincided only 51% of the time and differed by 2.2°C on average.

In summary, we analyzed studies that quantified the intrinsic rate of increase (*r*), net reproductive value (R_o), and generation time (T) at three or more temperatures.

For 77 of 78 species, the fitness curve for r was shifted to higher temperatures than that for R_o. This pattern appears to result from the sensitivity of r (but not of R_o) to the accelerating effect of high temperature on generation time. Also, the thermal dependence of development time is a better—though not perfect—predictor of the thermal dependence of r than is the thermal dependence of lifetime fecundity. These observations reinforce a well-known warning that the choice among fitness measures must be made with reference to the demography of the population under study, and it also cautions against using the thermal sensitivities of lifetime fecundity or even of development time as a surrogate for the thermal dependence of fitness (for populations in which r is in fact the appropriate measure of fitness). There is no robust shortcut for estimating the thermal dependence of fitness.

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