Comparative Thermal Physiological Ecology of Syntopic Populations of *Cacama valvata* and *Tibicen bifidus* (Homoptera: Cicadidae): Modeling Fitness Consequences of Temperature Variation

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SYNOPSIS. This paper develops a model based on egg-laying rates and female ovi-position temperature preferences in two species of cicada, *Cacama valvata* and *Tibicen bifidus*, from a central New Mexico desert grassland habitat. Output from the model indicates that *C. valvata* achieves maximal daily egg production (eggs female⁻¹ day⁻¹) on days when maximum shade ambient temperatures reach 41°C; the corresponding value for *T. bifidus* is 33°C. These differences correlate with the thermal regime experienced by each species in its respective typical habitat. Simulations of the effects of variation in mean habitat ambient temperature on egg production demonstrated that known distributional limits for *T. bifidus* correspond to thermal conditions that reduce daily egg production by only about 5-10% relative to long-term means at the study site. The same is true for *C. valvata* only in lower-ambient temperature habitats. In higher-temperature habitats, *C. valvata* exhibits an unusual plasticity in the timing of adult activity and reproduction that allows it to occupy a much wider geographic range than *T. bifidus*. Contrary to expectations, frequency distributions of predicted daily egg production rates were negatively skewed in each species’ respective ‘typical habitat’, and Gaussian only in thermally marginal habitats. The findings are discussed in the context of attempts to model population- and community-level effects of climatic change.

INTRODUCTION

A key to understanding evolution of physiological traits is to ascertain how variation in such traits affects components of fitness such as survival, energy acquisition, growth rates, mating success, and fecundity in the context of extant variation in relevant abiotic parameters (Bennett, 1987; Kingsolver, 1989; Huey and Kingsolver, 1989; Kingsolver et al., 1993). This is especially necessary if we are to take advantage of the promise that study of physiological traits holds for developing a "more predictive theory of evolution" (Watt, 1991).

Most studies of the ecological and evolutionary consequences of environmental variation have focused on ambient temperature (T_a) as the relevant variable (Dunham, 1993; Hoffmann and Blows, 1993). Ambient temperature is a particularly apt choice because the effects of variation in T_a are pervasive, especially for ectotherms, and the mechanisms of temperature’s impact on biological systems are understood (Hochachka and Somero, 1984; Prosser, 1986). In addition, the threat of global warming lends a sense of urgency to the need to understand how organisms will react to the sort of changes in T_a regime predicted by current models (Schneider, 1993; Hoffmann and Blows, 1993; Dunham, 1993).

Organisms respond to stress by evasion and/or resistance (Hoffmann and Parsons, 1991; Hoffmann and Blows, 1993), each of which has its own costs and benefits. In the case of thermal stress, the net effect of these costs and benefits has been selective pressures that have quite often led to the ability to exert control over body temperature (T_b). For the majority of animals, this control is usually achieved by behavioral means. However, while behavioral thermoregulation can be very effective, reliance on this strategy can impose time and energy constraints on ectotherms (Huey, 1990) and can...
limit their ability to prevent excessively high T_b (Dreisig, 1980; Kingsolver and Watt, 1983; Hadley et al., 1992; Dunham, 1993). This, in turn, can have significant impacts on the biochemical, physiological, individual, and population-level response of many ectothermic species to their thermal environment (Kingsolver, 1983; Kingsolver and Watt, 1983; Powers, 1987; Grant and Dunham, 1988, 1990; Watt, 1991; Hadley et al., 1992; Dunham, 1993).

During a 9-year field study of the thermobiology of syntopic populations of two species of cicada, Cacama valvata and Tibicen bifidus, it became apparent that the timing and duration of reproductive behaviors of males and females were affected by natural variation in daily T_a regime. For example, reproductive activity (singing, mating, and oviposition) in each species typically commenced early in the morning and ceased by late morning. However, on cool days, reproductive activity in both males and females was significantly delayed, peaking around 1400 hr in each species, and on very hot days reproductive activities ceased by mid-morning. These findings, coupled with other lines of evidence that variation in T_a has significant impacts on reproduction in cicadas (Hastings, 1989; Hastings and Toolson, 1991; Toolson and Toolson, 1991), led to the present investigation of the potential impact of this variation on fitness in C. valvata and T. bifidus.

Short-term (seconds to minutes) variation in abiotic conditions, especially solar radiation intensities and T_a, can adversely affect fitness in many ectotherms (Kingsolver and Watt, 1983; Dunham, 1993). However, cicadas' ability to avoid overheating by sweating and passive evaporation (Toolson, 1987) largely obviates the immediate impact of conditions that could drive T_b to dangerously high levels, and their ability to elevate T_b when T_a is low likewise allows them to keep T_b above the minimum required for activity under all but the very coolest conditions (Hastings and Toolson, 1991; Toolson and Toolson, 1991; Sanborn et al., 1992; Toolson et al., ms. submitted). As a result, although abiotic conditions at the study site threatened both C. valvata and T. bifidus with changes in T_b of as much as ±10–15°C over time scales of seconds to minutes, their thermoregulatory responses allowed oviposition to continue unabated during these intervals. Thus, in contrast with some other insect species (Kingsolver and Watt, 1983), I found no evidence that reproductive success of C. valvata or T. bifidus was adversely affected by such short-term variation in abiotic conditions. Instead, I believe that day-to-day fluctuations in T_a regime and changes in general T_a conditions from year to year are far more significant for both C. valvata and T. bifidus.

In this paper, I use data on temperature preferences and egg-laying rates of female cicadas as the basis for a model that estimates daily egg production rates in two species of cicada. I use this model to investigate the impact of natural day-to-day and year-to-year variation in T_a on mean daily egg production by females, and use this population-level fitness parameter to investigate the impact of natural variation in T_a on fitness in each species. I then evaluate the fitness consequences of changes in long-term mean habitat T_a. Output from the model indicates that each species' geographic distributional limits are defined by T_a conditions that correspond to surprisingly small reductions in mean daily egg production. The model also reveals that plasticity in life history traits—timing of adult activity and reproduction in this case—can significantly modify the impact of variation in T_a on fitness.

**MATERIALS AND METHODS**

**Field studies**

The studies were conducted in June from 1986 through 1994 at a site (elevation = 1,950 m) 20 km west of Socorro, NM. The habitat is desert grassland dominated by bunch grass (Muhlenbergia sp.), rice grass Oryzopsis sp., and a variety of herbaceous annuals. The predominant emergent plants are Yucca elata, staghorn cholla (Opuntia arborescens), Apache Plume (Fallugia acuminata), Thelesperma sp., Hymenopappus filifolia, (preferred oviposition host for T. bifidus at the study site) and Gutierrezia sp. (preferred oviposition host for C. valvata).
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Details of the techniques employed during the field work may be found in Hastings and Toolson (1991) and Toolson et al. (ms. submitted). In brief, data were obtained by randomly walking through the habitat occupied by C. valvata and T. bifidus and capturing every cicada detected. When a cicada was located, its behavior (ovipositing, singing, feeding or perching) was noted, after which it was captured and its thoracic temperature ($T_{th}$) was obtained as described in Hastings and Toolson (1991). Immediately afterward, the air temperature ca. 5 mm above the surface of the site occupied by the cicada when first observed was obtained and recorded as the site temperature ($T_{site}$).

Oviposition rates were estimated by locating females preparing to oviposit and recording the duration of each female’s oviposition bout. Using care not to disrupt oviposition, I recorded $T_{site}$ at 5-min intervals during each oviposition bout. As soon as a female concluded ovipositing, the plant stem(s) containing her eggs were individually marked and returned to the laboratory for counting of eggs.

Data on seasonal activity and distribution limits were obtained from field work and from specimens in collections at: The Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131; Department of Zoology, Arizona State University, Tempe, AZ 85281; Department of Entomology, Kansas State University, Manhattan, KS; Department of Bioagricultural Sciences and Pest Management, Colorado State University, Ft. Collins, CO 80523.

RESULTS

We gathered $T_{th}$ and $T_{site}$ data from a total of 244 C. valvata females and 392 T. bifidus females. As is the case with other cicada species (Hastings and Toolson, 1991; Toolson and Toolson, 1991), both C. valvata and T. bifidus made extensive use of behavioral thermoregulatory mechanisms throughout the day. In the early morning, cicadas were found in relatively warm microhabitats, but tended to move to relatively cool microhabitats as $T_s$ increased during the day. As a consequence, $T_{site}$ for females exhibited a linear dependence on shade $T_s$ (Fig. 1) that is described by the equations:

- **C. valvata**: $T_{site} = 0.644(T_s) + 10.69$; $r^2 = 0.65$  
  Equation 1a

- **T. bifidus**: $T_{site} = 0.771(T_s) + 7.39$; $r^2 = 0.76$  
  Equation 1b

The slope of each regression was significantly different from both 0.0 and 1.0 ($P < 0.0001$).

The proportion of cicadas engaged in reproductive behaviors as a function of $T_{site}$ was presented in Figure 2. Female C. valvata oviposited over a slightly wider range of $T_{site}$ than female T. bifidus, and exhibited higher oviposition frequencies at high $T_{site}$. In each species, the upper end of the frequency distribution was truncated by the response of females to increasing $T_{site}$.

In the case of T. bifidus, females interrupted oviposition and abandoned an oviposition site as soon as $T_{site}$ reached 33–35°C. Similarly, I found no female C. valvata engaged in oviposition unless $T_{site}$ was less than 37–38°C.

Estimated egg-laying rates by females of each species were independent of $T_{site}$ over the range from 23 to 38°C (linear regression analysis; $P > 0.5$), averaging 35.15 ± 2.50 eggs hour$^{-1}$ in C. valvata (n = 13) and 15.98 ± 1.61 eggs hour$^{-1}$ in T. bifidus (n = 30).

Effects of natural variation in ambient temperature on daily egg production

Modeling the effect of this variation in $T_s$ regime on C. valvata and T. bifidus populations required an ecological performance measure (sensu Huey, 1991). The unusual life cycle of cicadas, specifically an underground nymphal stage lasting several years, rendered nymphal growth or survival rates an impractical parameter. Therefore, I chose egg production as the fitness component to use in the model. Given the sophisticated thermal microhabitat selection ability of both C. valvata and T. bifidus (Fig. 1; Equations 1a and b; also Toolson et al., ms. submitted), I assumed that the $T_{site}$-dependence of oviposition frequency (Fig. 2) reflected the ‘suitability’ of various $T_{site}$ for...
FITNESS EFFECTS OF TEMPERATURE VARIATION

40
35
30
25
20

C. valvata

T. bifidus

Shade T (°C)

FIG. 1. Air temperature (TsiB) at sites occupied by female C. valvata and T. bifidus as a function of 1-meter shade ambient air temperature (T a).

Shade T (°C)

oviposition and elected to use the frequency of oviposition at different Tsite as the starting point for the modeling efforts.

Long-term meteorological records for the Socorro, NM municipal airport (located 20 km from the study site), were used to model the Ta regime experienced by C. valvata and T. bifidus at the study site. During the period of the study, maximum daily shade Ta recorded at the study site (Ta max) was accurately predicted (r² = 0.97; n = 19 days) by a linear model based on the daily maximum Ta recorded at the Socorro airport. Consequently, I was able to use the Socorro airport records to estimate daily Ta max at the study site for the interval June 14–30 from 1945 through 1991.

Between 1945 and 1991, Ta max at the study site for June 14–30 ranged from 20.7° to 40.7°. The overall (1945–91) mean Ta max for the June 14–30 interval was 32.95 ± 2.87°C (X ± SD), but the within-year mean Ta max for June 14–30 ranged from 29.3° to 37.1°C, and the average change in mean Ta max from one year to the next was ±1.6°C. Within years, the mean change in Ta max from one day to the next was ±1.6°C, and the change in Ta max from one day to the next exceeded ±5°C at least once during the June 14–30 interval.

For any given day, shade Ta during the cicadas’ active period was described quite well (r² = 0.95) by an equation of the form:

$T_{a,t} = T_{a,max} + a \sin[(t - b)/c]$

Equation 2

where Ta max, in this case was the maximum shade Ta for the day, and Ta,t is the shade Ta at time t.

Using Equations 1a and 1b, I solved for the values of T a required to yield the lower and upper limits for each of the 2°C Tsite intervals in Figure 2. Then, by solving Equation 2 for the values of t corresponding to each T a,t, I calculated the total amount of time that Tsite was within the limits of each Tsite interval in Figure 2. Each of the resulting times was then multiplied by the oviposition frequency for the corresponding Tsite interval, and the resulting products were summed over the interval from 0800–1800 hr (this time span was chosen to encompass the earliest and latest times that females were observed ovipositing during the 9 years of the study, with an extra 0.5 hr added on at each end). The units for this sum are female-hours/female/day, or simply hours/day. This number represents the number of hours in a day (with a given Ta max) during which females can engage in oviposition. Multiplying this number by the corresponding egg-laying rate for C. valvata and T. bifidus yielded estimated daily egg production by an “average” female of each species. These calculations were repeated for 1° intervals for Ta max between 20° and 51°, yielding an estimated Eggs/female/day value for each Ta max.

These results can be combined with the long-term Ta max data to model the potential effects of environmental variation on C. valvata and T. bifidus populations. I first ex-
estimated a long-term mean egg production by females of each species for the 1945–1991 interval by multiplying the respective species’ daily egg production for each $T_{\text{a, max}}$ by the frequency of that $T_{\text{a, max}}$ between 1945–91, and summing the products. This number represents the long-term mean number of eggs per day that an individual female of each species would be expected to produce (Table 1).

Frequency distributions of estimated egg production rates by $C. \text{valvata}$ and $T. \text{bifidus}$ females for the 1945–91 interval are presented in Figure 3 (for clarity of presentation, the individual daily egg production rates were grouped into “bins” of 10). In $C. \text{valvata}$, thermal conditions on most days (ca. 62% of total days) during the 1945–91 interval resulted in the production of 50–59 eggs/female/day. However, the suitability of days for egg production by $C. \text{valvata}$ females varied considerably, with some days being highly favorable and others unfavorable for oviposition. The result is a more-or-less symmetric frequency distribution, ranging from a low of 4.3 eggs/day ($n = 1$ day between 1945–91) to a high of nearly 109 eggs ($n = 2$ days). In contrast, more than 80% of the days between 1945–91 allowed $T. \text{bifidus}$ females to produce between 30 and 33 eggs/day (the maximum that $T. \text{bifidus}$ females produced in the simulation runs; Table 1). The result was a neg-

### Table 1. Estimated long-term mean egg production rates for $C. \text{valvata}$ and $T. \text{bifidus}$ between 1945 and 1991.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C. \text{valvata}$</td>
<td>56.4</td>
<td>5.61</td>
<td>4.3</td>
<td>108.6</td>
</tr>
<tr>
<td>$T. \text{bifidus}$</td>
<td>30.5</td>
<td>2.79</td>
<td>0.0</td>
<td>33.2</td>
</tr>
</tbody>
</table>
Effects of long-term changes in mean habitat temperature on egg production

The fitness consequences of change in habitat T_h regime were modeled by varying the long-term mean T_h from -6° to +12°C (2°C intervals) relative to the long-term mean T_h at the study site and repeating the calculations described in the previous section (analysis of long-term meteorological records for stations in Arizona, New Mexico, and Colorado revealed that the variance in daily T_{max} did not change with altitude, so variance in T_h was kept constant for these simulations). Results of this simulation are presented in Figure 4, in which egg production values are expressed relative to each species’ respective long-term mean at the study site (Table 1). The downward-pointing arrows indicate changes in mean T_h produced by altitude-latitude combinations at locations along the known distributional limits for T. bifidus, while the upward-pointing arrow indicates the same value for C. valvata in cool habitats (see Discussion).

The corresponding frequency distributions are presented in Figure 5. These graphs are similar to Figure 3, except that all Egg/female/day values for each species have been expressed as a percentage of the maximum value observed in each species’ typical habitat. In the case of T. bifidus, typical habitat thermal regime is similar to that at the study site (see Fig. 3), while the typical habitats for C. valvata average roughly 8°C warmer (+8°C). By expressing egg production rates relative to each species’ maximum, the frequency distributions are converted into fitness functions that facilitate comparison between species and across habitat thermal regimes.

**DISCUSSION**

**Key assumptions of the model**

The choice of egg production rates as the ecological performance measure was based on the assumption that realized fecundity plays an important role in driving dynamics of both C. valvata and T. bifidus populations across their respective geographic ranges. By extension, density-dependent factors such as predation, competition, and disease processes are assumed not to be preeminent in the regulation of C. valvata and T. bifidus populations. If density-dependent forces control C. valvata and T. bifidus populations, then variation in egg production rates might have little impact on population dynamics. However, many temperate insect species’ population dynamics do, indeed, reflect the ability of females to produce eggs, with population pressures and other biotic factors becoming important only under particular circumstances (Begon, 1983; Dempster, 1983; Cammell and Knight, 1992; Kindvall, 1995; Coxwell and Bock, 1995; Kingsolver, 1995; Tammaru et al., 1996). And, with respect to cicadas, Williams et al. (1993) and Williams and Simon (1995) highlighted the impact of climatic events—as opposed to population pressures and biotic factors—on populations of periodical cicadas (Magicicada spp). The assumed importance of realized fecundity awaits empirical verification in western cicada species, but available data suggest that it is a reasonable one.

A second assumption—that the long-term egg production rates represent replacement values—was made to facilitate the simulations of the impact of temperature variation on population fitness. However, if source-sink dynamics (Pulliam, 1988; Pulliam and Danielson, 1991; Dias, 1996) are operative in the study species, then the estimated long-term egg production rates might over- or underestimate the replacement values. Although empirical support for the operation of source-sink dynamics in nature is limited, and alternative models seem to be supported by much of the recently published data (Doncaster et al., 1997), this eventuality must be kept in mind when extending the simulation results to interpretation of, for example, range limits.

The model also makes the implicit assumption that the temperature-dependence of oviposition frequencies (Fig. 2) does not change over the range of C. valvata or T. bifidus. Acclimation or local adaptation of females’ response to temperature could modify or even obviate the impact of temperature variation on egg production rates.
Fig. 4. Effects of changing long-term mean $T_a$ on mean daily egg production by female *C. valvata* (○) and *T. bifidus* (●). Egg production rates are expressed relative to each species' respective long-term mean at the study site (Table 1). Arrows indicate changes in mean $T_a$ produced by altitude-latitude combinations at locations along each species' known distributional limits.

However, available data suggest that these are not options for cicadas. In the laboratory, cicadas do not exhibit significant thermal acclimation response (Toolson, 1994). Data from the cicada genus *Magicicada* over a broad latitudinal range has shown that adult emergence is triggered when soil temperature reaches a value that does not vary with latitude (Heath, 1967), and Andersen (1994) reported a similar phenomenon in *Diceroprocta apache*. Finally, populations of *C. valvata* and *Tibicen chiricahuana* show no evidence of local adaptation of thermobiology across an altitude range of 600 m, in spite of interpopulation differences in mean $T_{site}$ and mean $T_b$ of as much as 3–5°C (Toolson, unpublished).

**Fitness variation in *C. valvata* and *T. bifidus* populations at the study site**

In addition to significant differences in the long-term mean egg production rates (Table 1), the frequency distributions for *C. valvata* and *T. bifidus* differed qualitatively (Fig. 3). Under the thermal conditions characterizing the study site, the distribution for *T. bifidus* was negatively skewed, with the majority of days being clustered towards the high end of the distribution, meaning most days were favorable for oviposition for *T. bifidus*. In contrast, the distribution for *C. valvata* was nearly Gaussian ($r^2 = 0.97$). As a result, female *C. valvata* experience a greater variance in estimated daily egg production rates than female *T. bifidus* (Table 1), for whom most values are clustered near the long-term species' mean.

Daily egg production was reduced to ≤75% of the long-term mean by $T_a$ conditions during 14% of days for *C. valvata* but only about 4% of days for *T. bifidus*. However, no day gave an estimated egg production of 0.0 for female *C. valvata* but 3 days during 1945–91 did so for *T. bifidus*. Egg production exceeded 110% of the long-term mean during roughly 10% of the days for *C. valvata*, but this virtually never occurred in *T. bifidus*, reflecting the negative-
FIG. 5. Effect on C. valvata and T. bifidus fitness functions of decreasing or increasing long-term mean $T_a$ relative to the 1945-91 mean $T_a$ at the study site. Values on the x-axis represent daily egg production rates expressed as a percentage of each species' maximum egg production rate in its respective typical habitat; the thermal regime characterizing typical habitats for T. bifidus is similar to that of the study site (see Fig. 3), while the typical habitats for C. valvata average roughly 8°C warmer (+8°C).

ly skewed distribution of egg production frequencies. Presumably, C. valvata has persisted in the marginal habitat of the study site because the negative impact of the relatively high frequency of less suitable days is offset by exceptionally good days when egg production rates can be as much as twice the long-term mean.

In the simulations, large reductions in daily egg production for C. valvata were always the result of relatively cool days, and the hottest days ($T_{a,\text{max}} \geq 37^\circ\text{C}$) were associated with the highest egg production rates ($\geq 110\%$ of the long-term mean at the study site). This accords with expectations for a species typically found in hot desert habitats. In T. bifidus, however, very low relative egg production values occurred not only on the hottest days ($T_{a,\text{max}} \geq 39^\circ\text{C}$), but also on the coolest ($T_{a,\text{max}} \leq 25^\circ\text{C}$) days. The negative impact of very hot days was expected from the geographic and altitudinal distribution of T. bifidus but the sensitivity of T. bifidus to cold days—due to the fact that T. bifidus cannot readily elevate $T_a$ to active levels on cold days—was surprising.

Kingsolver's classic studies with Colias butterflies were among the very first to apply biophysical principles of heat exchange and thermoregulation to the question of how environmental variation affected fitness and, therefore population dynamics (Kingsolver, 1983, 1985). As in cicadas, butterflies can fly and engage in reproductive activity only if their $T_b$ is within acceptable limits. Unlike cicadas, however, butterflies can avoid overheating only via behavioral mechanisms. This renders them quite sensitive to short-term fluctuations (sec to min) variation in $T_a$ and solar radiation flux, and the consequence is a marked
degree of fluctuation in realized fecundity from day-to-day and year-to-year. Analysis of the data suggests that the variation in realized fecundity appears to play an important role in driving population dynamics of many temperature butterfly species (Kingsolver, 1989). Continued work with other butterfly species has demonstrated that traits associated with thermoregulatory function are subject to fluctuating selection pressures, depending on thermal conditions experienced by the adults (Kingsolver, 1995). Cicadas, with their remarkable ability to avoid overheating, probably experience less disruption of reproduction by variation in $T_a$ over time scales of sec to min, but their very short adult reproductive life span (probably only 2–5 days in the case of *C. valvata* and *T. bifidus*) undoubtedly leaves them very susceptible to the impact of day-to-day changes in $T_{a,max}$.

**Effects of changes in long-term mean ambient temperature**

We can interpret Figure 4 in the context of each species' preferred habitats and known distributional limits by applying the approximation that mean $T_a$ decreases 6°C for every 1,000 m increase in altitude or, in temperate latitudes, for every 7 degree increase in latitude (Ricklefs, 1973, and confirmed by analysis of data from meteorological stations in Colorado, New Mexico, and Arizona) to calculate expected changes in mean $T_a$ for habitats along the known distributional limits for each species. In *T. bifidus*, relative egg production was maximal under the $T_a$ regime at the study site. This result was not surprising.

Although sympatric over portions of Arizona, New Mexico, and Colorado, *C. valvata* and *T. bifidus* occupy generally different geographic ranges. *Cacama valvata* is widely distributed in xeric habitats from sea level to nearly 2,000 m throughout the southwestern United States and northern Mexico. The population on which the present work is based is thus near the upper altitudinal limit for *C. valvata* (M. Heath, personal communication; Hastings and Toolson, unpublished data). Over much of this range, *C. valvata* adults are active only during late June and early July. *Tibicen bifidus* is found in grassland habitats from western Kansas and eastern Colorado to southern Arizona and New Mexico, and is generally found in cooler habitats than *C. valvata*. The study site is typical *T. bifidus* habitat. Populations of *T. bifidus* have been recorded from altitudes as high as 2,100 m in Arizona and New Mexico (J. Hastings, personal communication; Toolson, personal observation), but have not been recorded below about 1,100 m to 1,500 m (southern New Mexico and Arizona; J. Hastings, personal communication; Toolson, personal observation). All collection records for *T. bifidus* across its geographic range are between June 7 and July 1.

The change in mean $T_a$ corresponding to the altitude limits for *T. bifidus* in central New Mexico/Arizona was calculated to be $+2\degree C$ (corresponding to an altitude of 1,600 m) and $-1\degree C$ (altitude = 2,100 m) relative to mean $T_a$ at the study site. The northernmost habitats occupied by *T. bifidus* are from northern NM (1–2 degrees N of the study site), where it occurs up to 2,100 m (equivalent to a decrease in mean $T_a$ of $\approx 3\degree C$ compared with the study site), to western Kansas (3–5 degrees N of the study site), where it can be found at altitudes as low as 1,000 m (equivalent to an increase in mean $T_a$ of $\approx 3\degree C$ compared with the study site). These results suggest that *T. bifidus* can only persist in habitats where the mean $T_a$ is within $\pm 3\degree C$ of the mean $T_a$ at the study site. The estimated egg production by *C. valvata* also declines with decreasing mean $T_a$. In central New Mexico, *C. valvata* does not occur above an altitude of 2,200 m (Hastings and Toolson, unpublished data), where the predicted mean $T_a$ is approximately $1.5\degree C$ less than at the study site. At the northern limit of its range in Colorado and Utah (3–5 degrees latitude north of the study site, equivalent to a $2.5\degree C$ to $4\degree C$ decrease in mean $T_a$ regime), *C. valvata* does not occur at elevations above 1,500 m. The lower altitude limit partly offsets the thermal effect of the
higher latitude, yielding a change in mean $T_a$ at the distribution limits of approximately $-1^\circ$ to $-2^\circ$C relative to the study site mean. Here too, predicted egg production rates at the distributional limits of $C. valvata$ are only slightly lower than at the study site.

However, over most of its range, $C. valvata$ occupies habitats that are warmer than the study site. In spite of this, $C. valvata$ adults still become active in late June, at least down to altitudes of 800 m (Heath et al., 1972; B. Kondrotieff, personal communication; M. Kolner, personal communication). $C. valvata$ thus does not show the clinal response to degree-day accumulation that is seen in many insects, including some cicada species (Heath, 1967; B. Kondrotieff, personal communication). As shown in Figure 4, the consequence of this time-invariance in adult activity is egg production rates that progressively increase at lower equivalent altitudes and reach a maximum when mean $T_a$ is increased by roughly 8° (equivalent to an altitude of 600 m).

In contrast with $T. bifidus$, $C. valvata$ is capable of shifting the timing of adult activity. Near Phoenix, AZ (altitude = 350 m, equivalent to a 10° increase in mean $T_a$) $C. valvata$ is active in late May and early June (M. Kolner, unpublished Master’s thesis, Arizona State University, and personal communication), while at sea level in northwestern Mexico, $C. valvata$ is active in late April (E. Toolson, unpublished observations). In other words, once mean habitat $T_a$ increases beyond the point that relative egg production rates begin to decline (Fig. 4), $C. valvata$ shifts its adult activity time to progressively earlier in the year, when $T_a$ is generally cooler—and egg production rates are correspondingly greater—than in late June. The life history of $C. valvata$ appears to respond to habitat $T_a$ regime in ways that maximize fitness over a wide geographical range. $Tibicen bifidus$ does not show the shift in timing of adult activity seen in $C. valvata$ and thus has a more restricted geographic and altitudinal range.

Why don’t $C. valvata$ populations from altitudes greater than 600 m shift activity to later in the year, when $T_a$ regimes are generally warmer—and predicted relative egg production would be correspondingly greater—than in late June? I believe that this option is precluded by the onset of the summer monsoon weather pattern, which typically commences in early to mid-July. The summer monsoon is characterized by frequent occurrence of late morning and early afternoon thunderstorms, and although cicadas are well buffered against fluctuations in $T_a$, the combination of hard rain, high wind velocities, and dramatic decreases in $T_a$ associated with thunderstorms can be devastating to reproductive activities and even survival of most southwestern U.S. cicadas (Williams et al., 1993; E. C. Toolson, unpublished observations). Moreover, the increase in mean $T_a$ between late June and July is only about 1–2°C, which probably would not increase mean egg production enough to offset the risks associated with activity during the summer monsoon.

Fitness variation in marginal populations

Relatively little is known about the impact of habitat variation on fitness in populations at the margins of species’ distributions. Yet, understanding this aspect of the biology of marginal populations seems crucial to number of current endeavors, including attempts to develop and implement strategies for conservation of endangered species. Figure 4 suggests that persistence of cicada populations is precluded in habitats whose thermal regimes produce only small decreases in mean fitness. This surprising finding led me to investigate how Figure 3 would change across a thermal gradient encompassing the thermal regimes encountered by $C. valvata$ and $T. bifidus$ over their respective geographic ranges.

Plots of the frequency distributions of daily egg production rates along a thermal gradient provide a detailed picture of the effects of changing $T_a$ regime on fitness in $C. valvata$ and $T. bifidus$ populations (Fig. 5). The fitness functions in Figure 5 do not change dramatically between thermal regimes where populations can persist and those where they cannot. In $T. bifidus$, the most salient correlate of the range limits ($\pm 3^\circ$; Fig. 4) is that the frequency of days allowing females to produce $\geq 90\%$ of their typical-habitat maximum has decreased...
from ca. 0.6 at ±2° to less than ca. 0.4 at ±4°. In *C. valvata*, reducing mean *T*ₐ increased the frequency of low-egg production days, but had little overall effect on the shape of the distribution. Increasing mean *T*ₐ, on the other hand, caused the *C. valvata* distribution to become progressively more negatively skewed until mean *T*ₐ was increased beyond 8°. Further increases, which led to decreased mean daily egg production, returned the distribution to a more symmetric pattern.

Based on the assumption that the response of ovipositing females to temperature (Fig. 2) would be "adapted" to the general *T*ₐ conditions in the center of their range, I had made the *a priori* prediction that the frequency distribution for egg production in a species' typical habitat would be more or less Gaussian. I.e., females would achieve moderate rates of egg production under the most frequently encountered *T*ₐ,max conditions in their typical habitat, and the deleterious population-level effects of relatively rare 'bad' days (little or no egg production) would be offset by occasional 'very good' days when egg production was much greater than average. I further predicted that the distributions would be positively skewed for marginal populations, where occasional days when conditions were highly favorable for oviposition would allow population persistence by just compensating for the more frequent days when egg production was reduced by sub-optimal thermal conditions.

Figure 5 clearly does not support the *a priori* predictions. Under thermal regimes characteristic of each species' respective typical habitat (i.e., "+8°C" for *C. valvata*; "Study Site Mean *T*ₐ" for *T. bifidus*), the majority of days allowed both *C. valvata* and *T. bifidus* to realize egg production rates ≥90% of maximal, resulting in a negative skewness—and a remarkable degree of similarity between the fitness functions. Symmetric distributions of daily egg production rates were seen only in thermally sub-optimal habitats (i) at or near the limits of *C. valvata*'s range or (ii) well beyond the limits of *T. bifidus*'s range. Positively skewed distributions were generated only in *T. bifidus*, and then only when mean *T*ₐ was increased well beyond values corresponding to distribution limits.

Why are the egg production frequency distributions negatively skewed in each species' respective typical habitat? The proximate cause is that significant reductions in each species' egg production in its typical habitat are the result of excessively hot and/or cold days that limit the number of hours during which females can oviposit. Such days are infrequent in each species' typical habitat and the majority of days allow egg production rates near the species respective maximum, leading to the negative skewness. In a more ultimate sense, the results suggest that the physiological/biochemical basis for females' response to temperature has evolved to produce a species-specific pattern of response to temperature (Fig. 2) that interacts with the pattern of *T*ₐ variation in each species' typical habitat in such a way that most days yield high rates of egg production.

Attempts to explain the role of abiotic factors in setting the distributional limits of organisms typically focus on the importance of extreme climatic events such a freezing temperatures, minimum or maximum temperature during a certain season, etc. (Muth, 1980; Hoffmann and Parsons, 1991). The assumption is that absolute tolerance limits of one or more ontogenetic stages are exceeded by the extreme event, leading to inability of the population to persist. The results of these simulations are certainly consistent with that explanation, however, the relevant "extreme climatic event" is not readily apparent. The underground nymphs are protected from freezing since they burrow well below the soil surface, and the adults do not suffer significant mortality from climatic extremes that vary in any predictable way across their geographic range.

A number of alternative hypotheses suggest themselves. Extreme events may be important in some groups, but species may differ with respect to the importance of extreme climatic events. Perhaps, in cicadas a 5–10% reduction in egg production rates coupled with what must be low egg-to-adult survival rates is sufficient to drive populations to extinction. Indeed, the correspon-
dence of range limits with surprisingly small reductions in egg production rates might stem from peripheral populations' being maintained by a combination of immigration and local reproduction, with small reductions in egg production being sufficient to reduce the combination of reproduction and immigration to levels that will not support population persistence. Alternatively, relatively small reductions in mean fitness might make populations susceptible to the impact of extreme climatic events. On the other hand, perhaps the extreme climatic events on which most workers have focused as limits to distribution of a number of plant and animal species are simply the most noticeable reflection of the more subtle factors described here.

Regardless of the explanation, the simulation results are consistent with the hypothesis that response to temperature of ovipositing females (Fig. 2) plays a pivotal role in establishing distributional limits in C. valvata and T. bifidus. Clearly, more field work needs to be done. In particular, data on daily egg production rates in marginal populations are needed. Nonetheless, a focus on extreme events as limits of species' distributions may not be appropriate in all cases.

Consequences of climatic change

An important implication of the results is that increases in mean $T_a$ on the order of those predicted by models of global climatic change (Schneider, 1993) will have significant effects on population biology of C. valvata and T. bifidus. Moreover, it appears that these effects will differ in the two species. With its apparent lack of plasticity in phenology, T. bifidus seems particularly vulnerable to climatic change. Only within a restricted zone, where climate change (i) decreases mean $T_a$ of habitats that are presently warmer than the study site or (ii) increases mean $T_a$ of habitats that are presently cooler than the study site, will fitness of T. bifidus increase. Under conditions obtaining over most of its present range, predicted changes in thermal regime will reduce relative mean daily egg production in T. bifidus to levels below that corresponding to present range limits (Fig. 4). It thus seems likely that climate change will cause local extirpations of T. bifidus populations over much of its present range. Indeed, the ultimate fate of T. bifidus would probably rest on its ability to locate and occupy suitable habitats. Depending on the time-scale of $T_a$ change and the response of its host plant species, T. bifidus might well face extinction.

On the other hand, it would seem that C. valvata would generally benefit from increases in mean $T_a$ over most, if not all, of its current range. Figure 4 indicates that C. valvata should experience increased fitness over much of its present range (including low-$T_a$ marginal habitats), and we would expect population densities to increase therein. In warmer (low-altitude) habitats, C. valvata could simply shift adult activity times as $T_a$ increased beyond the optimum for egg production. Finally, warming of habitats currently not occupied by C. valvata would probably allow ecological expansion.

Cicadas play significant roles in the structure and dynamics of both plant and animal components of the ecological communities of which they are a part. Many bird species and some (but not all) insectivorous small mammal species benefit reproductively from the ‘influx’ into the above-ground food web of consumable biomass that accompanies the emergence of adults (Anderson, 1977; Rosenberg et al., 1982; Krohne et al., 1991; Williams et al., 1993), and the guild structure of a community may be altered dramatically in response to the pulse of adult emergence (Anderson, 1977). Effects on plant growth (Karban, 1983) and even soil water potential in desert ecosystems (Andersen, 1994) have been demonstrated. Insofar as the life history and population dynamics of C. valvata and T. bifidus interact with those of other organisms in their habitat, each species’ response to climatic change could have significant ramifications at the community level.

Others have discussed a research agenda for addressing questions about the evolution of thermal adaptations and the ecological and evolutionary consequences of global climatic change (see papers in Kareiva et al., 1993). For example, Dunham (1993)}
used this approach to develop a model of the expected impact of climatic change on populations of the lizard, *Sceloporus merriami*, in southwest Texas. Using data on thermal physiology, behavior budgets, and thermal mapping of habitats to develop a individual-based model, he concluded that a 2–5°C increase in $T_a$ would increase average equilibrium $T_b$ enough to markedly reduce time available for feeding by growing juveniles. An important conclusion of Dunham’s paper was that the impact of $T_a$ increases on reproductive success of year-old *S. merriami* would almost certainly lead to local extinctions. However, while such conclusions may be adequate for species with little or no plasticity in the timing of reproduction or other life-history traits (e.g., *S. merriami* or *T. bifidus*), my simulations suggest that other outcomes are probable for species with the requisite life-history plasticity.

I believe that the consequences of interspecific differences in life-history traits and plasticity thereof have not received the theoretical or empirical attention that they merit (however, see Ives and Gilchrist, 1993). These differences can be profound, even in phylogenetically and trophically closely related species. Note, for example, that *C. valvata* is clearly different from *T. bifidus* in that it can persist in habitats where estimated egg production rates are decreased markedly below the typical-habitat maximum (Fig. 4). The explanation for the ability of *C. valvata* to persist over a geographic range that imposes such large changes in realized fecundity is not apparent.

Focus on range shifts and/or local extinctions as likely responses to climate change may not lead to adequate models of the community- and ecosystem-level impacts of climate change. Life-history plasticity must be incorporated into any models of the ecological consequences of climatic change, especially when key species in a community differ significantly in this regard. Otherwise, our ability to make predictions about the nature and magnitude of the biological effects of climatic change on the dynamics of communities or ecosystems will be seriously compromised.

Finally, the natural inclination, when seeking to understand phenomena such as extinctions, population extirpations, and distributional limits, or when attempting to predict the effects of a particular perturbation such as climatic change, is to look for dramatic events or changes. However, it is becoming apparent that ecological communities can often exhibit complex, non-linear dynamics, with some small perturbations being amplified (e.g., by biotic interactions) all out of proportion, while other perturbations are completely damped out. Thus, Brown *et al.* (1997) reported that a modest change in winter precipitation sustained over two decades led to a dramatic (and unpredictable) reorganization of a desert community in the southwestern United States. Given that something as dramatic as species distribution limits may be generated by a 5–10% reduction in mean fitness (Fig. 4), it is perhaps not surprising that ecological communities can respond in non-linear ways to small perturbations.

Hoffmann and Blows (1993) have highlighted the need for an understanding of what determines limits to species distributions, which the results of my simulations suggest may be subtle. The recent report of a latitudinal cline in population extinctions of the endangered butterfly, *Euphydryas editha*, in the western United States (Parmesan, 1996) lends a sense of urgency to the need to understand what drives the dynamics of marginal populations. Unfortunately, data that explicitly address the patterns of realized fecundity in marginal populations of any plant or animal species have yet to be published. Such data are sorely needed, because peripheral populations are often the first to show symptoms of deleterious impacts of environmental change.

The approach described in this paper could be readily adapted for application to a wide range of systems. Empirical and model-based tests of the generality of the patterns presented in Figures 3 through 5 seem of particular interest. The implications of those results for conservation efforts will, I believe, be profound.

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