

INTERACTION OF TEMPERATURE AND RESOURCES IN POPULATION DYNAMICS: AN EXPERIMENTAL TEST OF THEORY

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ABSTRACT

Much debate in ecology has focused on the roles of density-independent factors (e.g. temperature) and density-dependent factors (e.g. resources) in regulating populations of animals, particularly ectotherms. I incorporate parameters expressed as general functions of temperature into a simple mechanistic model of resource-limited population growth. This model predicts that increased temperature should lead to greater density-dependent per capita mortality rates and lower equilibrium densities. I tested these predictions in a field experiment by monitoring mortality in grasshopper (Orthoptera: Acrididae) populations stocked at different densities in replicate cages and subjected to one of three different thermal treatments (shaded, control, or greenhouse). With increased temperature, per capita mortality rates were significantly higher and grasshopper densities at the end of the experiment were significantly lower. Increased temperature was associated with increased density-dependent mortality but not density-independent mortality. These results support the predictions of the model. In addition, strong interactions between temperature and resources may make species' populations more sensitive to thermal environmental change than would be expected from species' thermal tolerances.

Key words: temperature, density dependence, resource-limited population model, Acrididae, environmental change



Introduction

Ecologists have strongly debated the role of biotic versus abiotic factors in controlling the dynamics of populations. These factors have been strongly associated with the types of mechanisms limiting population growth: density dependence (Nicholson and Bailey 1935; Lack 1954) or density independence (Davidson and Andrewartha 1948; Andrewartha and Birch 1954). Proponents of density dependence have argued that per capita population growth rates decline with population density and that populations are controlled by competition or predation interactions (Lack 1954; Hutchinson 1978; Hanski 1990). Proponents of density independence have argued instead that per capita population growth rates are largely controlled by abiotic factors such as weather (Andrewartha and Birch 1954; Lawton and Strong 1981; Strong *et al.* 1984). Despite early ideas and experiments that linked abiotic factors and biotic interactions (Lotka 1925; Park 1954), the traditional view has been that the two types of factors are mutually exclusive.

Studies during the past 20 years strongly suggest that abiotic and biotic factors are not mutually exclusive and are likely to interact (Magnuson *et al.* 1979; Kingsolver 1989; Tracy 1992). Many physiological and behavioural processes that directly determine organisms' ability to gather and compete for limiting resources or to exploit prey depend on an abiotic factor, environmental thermal conditions (Magnuson *et al.* 1979; Gates 1980; Porter 1989). Thus, thermal conditions probably have strong effects on the outcome of density dependent interactions (e.g. competition, predation) for many species (Dunham 1993). Chesson (1990, 1994) and Pacala and Tilman (1994) use these relationships to show that interaction between abiotic factors and biotic interactions may help explain population persistence and species coexistence in competitive environments. Despite these ideas, the interaction between temperature and density dependent interactions has generally not been explored in theoretical studies (Tracy 1992; *cf.* Ives and Gilchrist 1993), and few specific hypotheses exist.

Thermal conditions and biotic interactions are most likely to be linked for ectotherms, because their metabolism, locomotion, and physiological processing of resources are sensitive to their thermal environment (Kingsolver 1989; Dunham 1993). Resource acquisition, metabolism, and conversion of resources into growth and reproduction all change predictably with temperature for ectotherms (Porter 1989). These typical functions are based on temperatures measured in black-body laboratory environments, but the effect of the complete array of thermal factors characteristic of realistic environments, including radiation and convection, can be incorporated by considering temperature to be T_p , standard operative temperature (Porter and Gates 1969; Bakken 1976; Gates 1980). General expressions of resource intake, metabolism and conversion for ectotherms as a function of temperature (Porter 1989) can be incorporated in simple models of population dynamics (Schoener 1973; Lomnicki 1988) to reveal some general predictions about the interaction between thermal conditions and resources in limiting population dynamics.

One case where temperature is likely to interact with resources in affecting population dynamics is for strictly resource-limited populations (*sensu* Schoener 1973), i.e. where a fixed supply of resource, S , must be shared by all individuals in the population. These resources must be spent on requirements for maintenance at a rate $m(T)$ and remaining resources are then converted into growth or reproduction at a rate $c(T)$. These rates are expressed as functions of temperature, T , to reflect their potential temperature-dependence. In continuous time, the dynamics of such a population can be expressed as

$$\frac{dN}{dt} = Nc(T) \left[\frac{S}{N} - m(T) \right] \quad (1)$$

where N is population size or density. In this simple model, the per capita rate of increase, r , is

$$r = c(T)S/N - c(T)m(T) \quad (2)$$

and the carrying capacity or equilibrium density is

$$K = \frac{S}{m(T)} \quad (3)$$

The change in these characteristics with temperature depend on the typical shapes of the functions $c(T)$ and $m(T)$. For the majority of ectotherm species and their environments, $c(T)$ is a constant (Porter 1989). This follows because conversion efficiency is not a rate; it depends more on the biochemical forms involved during growth and reproduction rather than on rate-dependent reactions (Calder 1984). Requirements, $m(T)$, should increase with temperature at an increasing rate (the familiar Q_{10} effect; Porter 1989). Consequently,

$$\frac{\partial c(T)}{\partial T} = 0, \quad \frac{\partial m(T)}{\partial T} > 0 \quad (4)$$

From these assumptions, per capita mortality and equilibrium density should change with temperature in the following way:

$$\frac{\partial r}{\partial T} < 0, \quad \frac{\partial K}{\partial T} < 0 \quad (5)$$

An explicit assumption of these predictions is that $\partial S/\partial T = 0$, i.e. that resource supply rate does not change with temperature. In addition, these predictions apply only if the population is resource limited; if per capita population growth is limited by time for resource consumption or digestive capacity, changes in r and K with temperature may be different (Schoener 1973, M. Ritchie unpublished).

In this paper, I test these predictions when applied to experimental populations of a common North American grasshopper *Melanoplus sanguinipes* (Orthoptera: Acrididae). This insect, a herbivorous univoltine ectotherm, typically hatches at high densities, declines throughout the summer, and reaches an equilibrium density in late summer (Belovsky 1986; Schmitz 1993; Joern and Klucas 1993; Ritchie and Tilman 1993). They are easily established in temporary 'microcosm' field cages, in which their initial densities are known and their subsequent dynamics can be easily measured. In most cases, these grasshopper populations appear to be limited by the supply of digestible plant material. For the grasshoppers in this experimental system, mortality occurs daily (i.e. continuously), there are no births, and resource requirements depend on grasshoppers' allocation of resources to survival versus growth or reproduction. Under these assumptions, resource requirements include resources spent on maintenance, growth, and reproduction, and mortality results when resource requirements exceed per capita resource availability. Furthermore, $r < 0$ because there are only deaths and no births, and increased temperature is likely to increase mortality rate μ (where $\mu = -r$). Equilibrium densities (K) should result when densities decline so that per capita resource availability equals demand and mortality rate is zero.

These assumptions were applied to the basic resource-limited population dynamics model (Eqn 1) and its associated predictions (Eqn 5) to generate three hypotheses which could be tested by this grasshopper system;

1. Resource supply rate does not change with temperature.
2. Per capita mortality rate is greater at higher temperatures.
3. Equilibrium densities are lower at higher temperatures.

These hypotheses were tested using a field cage experiment with differing densities of grasshoppers and three thermal environment treatments designed to determine if increased temperature affected population characteristics in the manner predicted by Eqn 5.

Methods

The study was conducted from June – August 1994 at the Millville Animal Research facility of Utah State University, located 10 km south of Logan, Utah. Experimental cages (see below) were placed on a dryland pasture (elevation 1393 m) with gravelly soils at the foot of the Bear River mountain range. The pasture was grazed in spring, but cattle had been removed by 15 June. Vegetation was non-native grassland dominated by the grasses *Bromus inermis* and *Agropyron cristatum*, bindweed (*Convolvulus arvensis*), and alfalfa (*Medicago sativa*). The grasshoppers *M. sanguinipes*, *Melanoplus femur-rubrum*, *Melanoplus confusus*, and *Camnula pellucida* were the dominant large insect herbivores at the site.

The effects of temperature on population dynamics were tested using a randomised two-factor design experiment, with grasshopper density and thermal environment the main effects on grasshopper mortality and final density. Sixty-three window-screen cages (40 × 40 cm base, 1 m tall, inserted 5 cm into the soil) were placed on the pasture in a 7 × 9 grid, with cages separated by 5 m (cf. Belovsky 1986; Ritchie and Tilman 1992; Schmitz 1993). After clearing the inside of cages of all large arthropods, cages were sealed at the top with binder clips. On 30 June, blue polyester tarpaulin covers (1.8 × 1.2 m) were erected on wooden frames mounted on steel posts over 21 of the 63 cages, such that they shaded cages from 1000–1400 hr. Over another 21 cages, 1.8 × 1.2 m wooden frames covered with clear polyethylene sheets were mounted on steel posts to create miniature greenhouses over cages. The remaining 21 cages were left as controls.

Standard operative temperature (T_r), a measure of the actual thermal environment experienced by organisms, is defined as the temperature in a black-body environment (Gates 1980; Vispo and Bakken 1993) that produces the same heat flux or body temperature of a grasshopper experiencing solar radiation, radiation from surrounding objects, and convection in a real environment.

Operative temperatures in dried mounted grasshopper nymph models were measured at half hourly intervals from 0600–2100 hr each day during the first four days of the experiment in three randomly selected cages from each thermal treatment (a total of 9 cages). This indirect method was used because body temperatures of live grasshoppers are extremely difficult to measure in the field (Bakken 1976; Chappell 1982). A needle thermistor probe was inserted into the grasshopper nymph model and connected the probe to a BHR® E-5 platinum digital thermometer, to obtain four separate, stable ($\pm 0.1^\circ\text{C}$ over 1 min) readings over 5 mins. At each reading, the model was positioned 2 cm above the ground, touching plant leaves or stems, at a different random location.

Prior to stocking cages, total nymphal densities of all species were measured as $32.4 \pm 8.3 \text{ m}^{-2}$ (S.E.) on 3 July from ten 0.5 m diameter ring counts (Capinera 1987) at random locations throughout the experimental grid. On 5 July, seven densities of 2, 3, 4, 6, 9, 12, and 16 third to fourth instar nymphs of *M. sanguinipes* were released per cage with three replicate cages for each thermal treatment. This provided initial stocking rates of 12.5, 18.7, 25, 37.5, 56.2, 75, and 100 nymphs m^{-2} . Grasshoppers for each cage were weighed collectively prior to release.

The number of grasshoppers in each cage was counted at 1, 3, 5, 8, 13, 18, 21, 25 and 31 days after stocking. Final densities were achieved when numbers of grasshoppers had remained constant in each cage for at least 10 days. After final counts, the remaining grasshoppers were removed from the cages and all green plant material inside each cage was clipped, dried at 45°C , and weighed. This material was then ground in a Wiley Mill through a 0.6 mm mesh screen, redried, and digested *in*

vitro in 2 g L^{-1} pepsin and 0.1 N HCl for 48 h at 38°C (Terry and Tilley 1964; Belovsky and Slade 1995). The percent of material digested estimates the dry matter digestibility of green plant material to herbivores. An index of food abundance for grasshoppers in each cage was obtained by multiplying green biomass and *in vitro* dry matter digestibility for each cage.

The per capita mortality rates (μ , where $\mu = -r$, from Eqn 2), were estimated by fitting the grasshopper declines in each cage to the following equation, obtained by solving Eqn 1:

$$N(t) = N_f - (N_f - N_0) \exp(-\beta t) \quad (6)$$

where N_f is final density observed in the cage, N_0 is initial density in the cage, t is time since the beginning of the experiment and β is an estimated regression parameter that corresponds to the product $cm(T)$ in Eqn 2 (c is assumed to be constant with temperature) for the per capita mortality rate. The final density was assumed to represent a within-season equilibrium within cages (Fig. 2), so $K = S/(m(T)) = N_f$, and as the initial mortality rate was being estimated, so $N = N_0$. After making these substitutions in Eqn 2 and simplifying,

$$\mu = \beta (1 - N_f/N_0) \quad (7)$$

All statistical analysis was performed with SPSS 6.1 for Macintosh® statistical package. The food-limited population growth model was fitted to the grasshopper dynamics within cages and β was estimated with non-linear regression. Differences in operative temperature among thermal treatments were analysed with repeated measures ANOVA. Differences in the parameter β , per capita mortality rates, and final densities were tested with two-way ANCOVA, with the final food abundance index as a covariate. Density-independent and density-dependent mortality rates were estimated for each thermal treatment from the intercept and slope, respectively, of linear regressions of per capita mortality rate against initial grasshopper density, with individual cages for each thermal treatment as sample points. Effects of initial grasshopper density and thermal treatment on green biomass, digestibility, and final food abundance were analysed with two-way ANOVA. All comparisons of means following ANOVA or ANCOVA were performed with Fisher's LSD test ($\alpha = 0.05$).

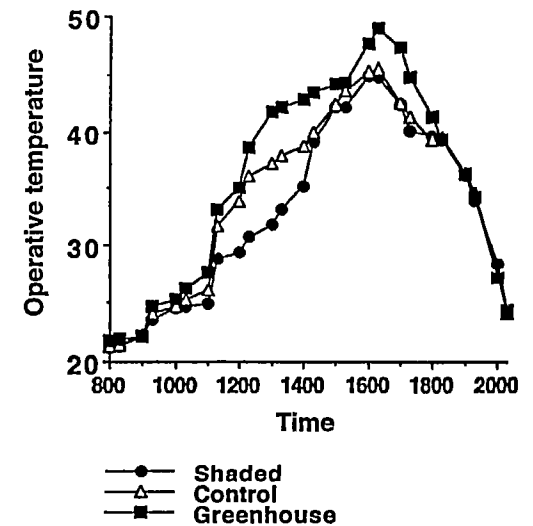


Fig. 1. Mean standard operative temperatures ($^\circ\text{C}$) measured inside grasshopper cages subjected to different thermal treatments (shaded, control, and greenhouse) during daylight hours over three days during the experiment.

Results

Operative temperatures differed significantly among thermal treatments ($P = 0.005$) especially during the period 1100–1500 hr (Fig. 1). Daytime (0700–2100 hr) average operative temperatures in each treatment were 33.0°C in shaded cages, 34.8°C in controls, and 36.2°C in greenhouse cages. The window screen cages used in this experiment were cooler by an average of 1°C of operative temperature than similar locations for grasshopper models outside cages.

Green plant biomass at the end of the experiment averaged $110 \pm 20 \text{ g m}^{-2}$ (S.E.) and did not differ among treatments ($P > 0.74$). *In vitro* digestibility of green plant material averaged $39.7 \pm 1.2 \%$ and also did not differ among treatments ($P > 0.22$). Consequently, the product of green biomass and digestibility in each cage at the end of the experiment (final food abundance) also did not differ among treatments ($P > 0.74$) and averaged $42.4 \pm 7.9 \text{ g m}^{-2}$.

Numbers of grasshoppers typically declined rapidly for the first 5 days but varied little over the final 18 days of the experiment (Fig. 2). Declines of grasshoppers within each cage fit the non-linear function in Eqn 6 very well ($0.85 < r^2 < 0.99$). The parameter β (Fig. 3a), which corresponded to an estimate of the product of conversion efficiency and resource requirements, correlated positively with final food abundance ($P = 0.05$) and negatively with final grasshopper density ($P = 0.02$). After controlling for these effects, β differed significantly with thermal treatment ($P = 0.04$) and initial grasshopper density ($P = 0.004$), but the interaction term was not significant. As expected from the results for β , initial per capita mortality rate also correlated positively with final food abundance ($P = 0.02$). It also differed significantly with thermal treatment (Fig. 3b, $P < 0.001$) and initial grasshopper densities ($P < 0.001$), but the interaction term was not significant. Overall, β and mortality rate increased with average temperature across the thermal treatments, which increased significantly between shaded and greenhouse cages (Fig. 3a,b). Densities of grasshoppers over the final 10 days of the experiment did not change in most cages (Fig. 2) and thus, final density reflected this stable density. Final density correlated negatively with final food abundance ($P = 0.05$), varied significantly among thermal treatments (Fig. 3c, $P < 0.001$) and increased with initial grasshopper densities ($P < 0.001$). The interaction was not significant.

For each thermal treatment, per capita mortality rate regressed significantly and positively with initial grasshopper density for all three thermal treatments (Fig. 4a) (shaded: $r^2 = 0.37$, $N = 21$,

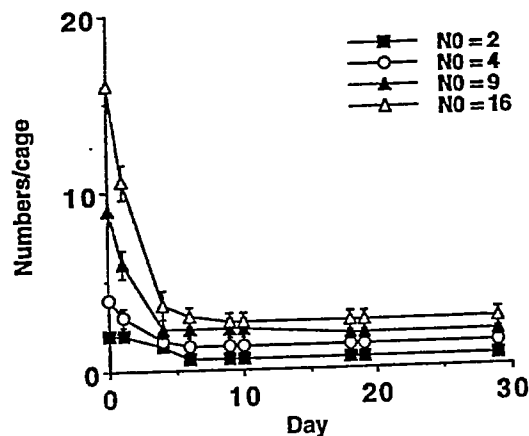


Fig. 2. Example trajectories of grasshopper numbers per cage over time after the beginning of the experiment (Day). Data are means (\pm S.E., $n = 3$) for control cages at four different initial stocking rates (NO: 2, 4, 9, and 16 per cage).

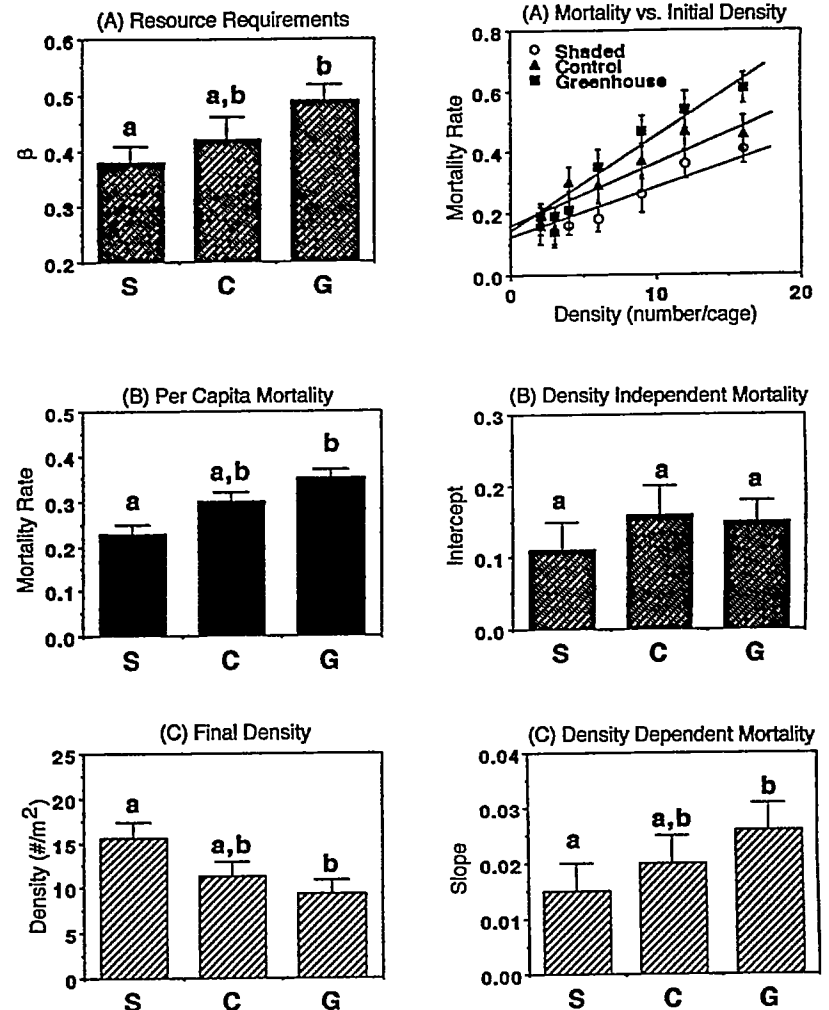


Fig. 3. Effects of thermal treatment (S, shade; C, control; G, greenhouse) on (A) the parameter β (rate of decline) which was estimated by fitting the resource limited population model (Eqn 1) to the trajectory of grasshoppers/cage over time, (B) calculated per capita mortality rate, and (C) final density. Values are means (\pm S.E., $n = 21$) pooled over all initial stocking densities for each treatment. Differences in lower case letters indicate significant contrasts.

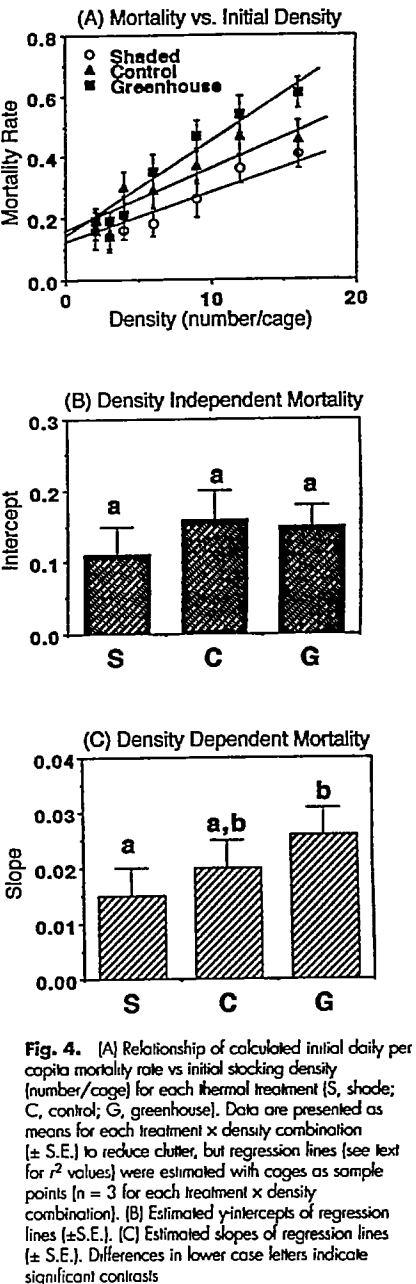


Fig. 4. (A) Relationship of calculated initial daily per capita mortality rate vs initial stocking density (number/cage) for each thermal treatment (S, shade; C, control; G, greenhouse). Data are presented as means for each treatment \times density combination (\pm S.E.) to reduce clutter, but regression lines (see text for r^2 values) were estimated with cages as sample points ($n = 3$ for each treatment \times density combination). (B) Estimated y-intercepts of regression lines (\pm S.E.). (C) Estimated slopes of regression lines (\pm S.E.). Differences in lower case letters indicate significant contrasts.

$P = 0.004$; control: $r^2 = 0.45$, $N = 20$, $P < 0.001$; greenhouse: $r^2 = 0.47$, $N = 21$, $P < 0.001$). The intercepts of these regressions did not differ significantly (Fig. 4b), but the slope of the regression for greenhouse cages was significantly greater than that for shaded cages (Fig. 4c).

Discussion

The results suggest that density dependent components of population dynamics in resource limited invertebrate populations may be affected by temperature. Specifically, the simple model of food limited population growth (Eqn 1) successfully predicted responses of per capita mortality rate and population density to temperature (Eqn 5). However, density independent mortality exhibited little change with temperature, which suggests that temperature had stronger effects on density dependent mechanisms than on density independent ones.

Temperature effects on mortality and density

The pattern of grasshopper decline in each cage (Fig. 2) fits well with that expected (Eqn 6) for a purely resource limited population (Schoener 1973). The basic model (Eqn 1) however, predicts that final grasshopper density should be constant with respect to initial density, in this experiment final density increased with initial density (Fig. 2). Although explanations other than the simple resource-limited population model are needed to fully describe the observed dynamics (see below), grasshoppers still appeared to be resource-limited. For a simple food limited system in which resource and consumer dynamics are explicitly modelled (see Appendix), equilibrium resource density, R^* , should be inversely related to equilibrium consumer density, N^* , because $R^* = S/(aFN^*)$, where a is the consumption rate of resource per unit time per unit resource and F is time for feeding each day. Since $N^* = N_f = S/m(T) = cS/\beta$, then $R^* = \beta/aFc$. These predictions suggest the following expected patterns: i) a positive correlation between final density and final food abundance, ii) a negative correlation between final density and final food abundance, and iii) a negative correlation between β and final density. All these patterns were observed in the data, so the simple resource-limited population growth model (Eqn 1) to predict the response of grasshopper populations to temperature described both grasshopper and plant dynamics under the controlled conditions within cages. This conclusion might not apply outside the cages as predators or habitat heterogeneity might reduce the influence of food limitation for grasshoppers.

As expected from the typical relationship between metabolism and temperature (Porter 1989), β increased significantly with operative temperature across the thermal treatments. Per capita mortality rate in the resource limited model is predicted to be directly proportional to b (Eqns 2 and 7), and, as expected from the results for β , also increased significantly with operative temperature. These patterns strongly support the prediction of Eqns 2 and 5, that per capita mortality rate should increase with temperature because resource requirements increase with temperature.

Densities in most cages were virtually constant during the final 10 days of the experiment, and probably reflected a within-season equilibrium in the absence of other factors that affect uncaged grasshoppers. Equations 3 and 5 predict that equilibrium density should decrease with an increase in temperature because resource requirements increase and fewer individuals can be supported by available resources. The fact that final density declined with increased temperature across thermal treatments (Fig. 3c) strongly supports this prediction. The increase in β across thermal treatments suggests that the pattern of final density may have been due to increased resource requirements with temperature.

An alternative hypothesis to explain these results is that the thermal treatments affected resource supply, S , or resource availability (final food abundance) and therefore grasshopper mortality rate and final density (Eqns 2 and 3). However, final plant biomass, *in vitro* digestibility, and food abundance in the experiment did not differ among thermal treatments. According to the resource-

limited model, final density ($N_f = cS/\beta$) (see Appendix). Thus, the product ($N_f\beta$) for each cage should be proportional to S for that cage, since c is assumed to be a constant. The product ($N_f\beta$) did not differ significantly between thermal treatments, again suggesting that resource supply was constant across thermal treatments. Therefore, the effects of temperature on resource requirements (β), and its consequences for per capita mortality rate and final grasshopper density, seems to be the most likely mechanism driving the experimental results.

For a given thermal treatment, both β and final density increased significantly with initial grasshopper density, even though the model predicts them to be constant. The results for β suggest that resource requirements increased with initial density. Individual grasshoppers may have increased their allocation of resources to growth and or reproduction in response to density, i.e. exhibited plastic life history shifts in response to a higher expected mortality rate (Monk 1985; Sanchez *et al.* 1988). Alternatively, greater interference among individuals with greater densities of grasshoppers could have caused individual grasshoppers to increase their activity and therefore their resource requirements. The pattern for final density is perhaps best explained by initial density independent mortality within the experiment (see below, Fig. 4a). With density independent mortality, even cages with initial densities near equilibrium will experience some mortality, thereby yielding a final density below equilibrium. Thus, only cages that begin at densities well above equilibrium should actually achieve the predicted equilibrium density. These discrepancies suggest that the overall population dynamics of these grasshoppers are more complex than those predicted by the simple resource-limited model. However, they do not detract from the patterns in mortality rates and final densities that support the simple model's predictions.

The experiment suggests that temperature and density effects interact. Although no significant interaction between the effects of thermal treatment and initial density was detected for any response variable with ANOVA, more detailed analysis shows that higher temperatures intensified density dependent effects. Per capita mortality rate was clearly density dependent (Fig. 4a), and the per capita density dependent mortality rate (slope of the regression between mortality and density) increased significantly with temperature (Fig. 4c). However, density independent mortality (the intercept of the regression) did not differ with temperature (Fig. 4b). These results suggest that temperature actually had its greatest effect on a density dependent component of population dynamics, which contradicts the traditional view that abiotic factors primarily affect populations in a density independent manner (Andrewartha and Birch 1954; Lawton and Strong 1981; Strong *et al.* 1984). Effects of temperature on density-dependent components may apply particularly within the upper and lower lethal temperature limits of organisms by affecting resource requirements and acquisition rates. The stronger the density-dependent effects in controlling population dynamics, the stronger the response to temperature is likely to be. Temperature may affect populations in a density independent manner when temperatures exceed lethal limits.

Other Implications

Numerous ecological models predict that temperature can affect population stability. For ectotherms, increased temperature should increase per capita mortality rate and/or resource requirements, either of which may decrease the likelihood of population stability (May 1974; Lomnicki 1988). These predictions could not be tested explicitly in this short-term study. Nevertheless, increased temperature is known to destabilise realistic simulation models of ectotherm population dynamics (Logan and Hilbert 1983; Wollkind *et al.* 1988; Doveri *et al.* 1993), and numerous insect populations exhibit dynamics that approach limit cycles and chaos in the absence of other factors (Turchin and Taylor 1992; Ellner and Turchin 1995). Given that a 40% increase in per capita mortality rate was associated with a 3°C increase in average daytime operative temperature in my experiment, it seems reasonable to expect that small temperature changes might have large effects on the stability of ectotherm populations.

Results from this and other studies suggest several implications of temperature–resource interactions for applied problems. Anthropogenic influences on ecosystems (e.g. agriculture, greenhouse gas emission, deforestation, urbanisation, etc.) often produce large, rapid changes in the thermal environment. Such changes are usually thought to impact species by producing conditions that exceed species' tolerance levels (Peters 1992). Species' persistence may be much more sensitive to changes in the thermal environment than expected from these tolerances; small changes in temperature within non-lethal bounds may influence extinction rates through the demographic or deterministic mechanisms described. Strong temperature–resource interactions may increase this sensitivity. No studies known to me have predicted an association between sensitivity of population stability and strong temperature \times resource interactions. Ives and Gilchrist (1993) and Ives (1995) argue that density dependence should ameliorate the effects of environmental changes such as temperature, but, they assume that density dependence and temperature effects act on different components of population growth and do not interact.

The experiment presented here supports the predictions (Eqn 5) of a simple model of population dynamics in which resource utilisation is temperature dependent (Eqn 1), and suggests that temperature may affect density dependent components of population dynamics more strongly than density independent ones. Support of these predictions occurred largely because the experimental system met most of the assumptions of the model, i.e. that caged grasshopper populations were resource limited, resource supply rate and availability was not affected by temperature, and no other factors, e.g. predation, affected the population. Therefore, this study does not show whether such interactions are important for real populations. It suggests, however, that considering the interaction of temperature and resources may greatly improve our understanding of the sensitivity of population dynamics to environmental change.

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Appendix

The simple resource-limited model for growth of a single consumer population (Eqn 1 in the text) actually arises from a trophic model of the dynamics of both the consumer and its resource. In its simplest form, this model assumes that the consumer, with density N , has a simple functional response, $f(R)$ and that the resource, with density R , is supplied at a constant rate S . Thus:

$$\frac{dR}{dt} = S - f(R)N$$

$$\frac{dN}{dt} = cN[f(R) - m] \quad (\text{A1})$$

where c is conversion efficiency and m is resource requirements for the consumer. The simplest functional response (Type I) is $f(R) = aFR$, where a is a constant that represents the search rate (area/time) of the consumer and F is time available for search within the period dt (e.g., time per day). We can also define the product cm as the parameter β , which was estimated in the field experiment. By making these two substitutions, we arrive at

$$\frac{dR}{dt} = S - aFRN$$

$$\frac{dN}{dt} = N[caFR - \beta] \quad (\text{A2})$$

A population is only strictly resource-limited (i.e., individuals share a fixed supply of resources) when the resource is at equilibrium (Schoener 1973). Solving for R at equilibrium yields $R^* = S/(aFN)$. Substituting R^* in the equation for consumer dynamics yields, the following equation, which is equivalent to Eqn 1 in the text.

$$\frac{dN}{dt} = N\left[\frac{cS}{N} - \beta\right] \quad (\text{A3})$$

When both consumer and resource are at equilibrium, the expected relationships between final grasshopper density (N^*), food abundance (R^*), resource requirements (included in β), search rate (aF), and resource supply (S) are:

$$R^* = \frac{S}{aFN^*} = \frac{\beta}{aF}$$

$$N^* = \frac{cS}{\beta} \quad (\text{A4})$$

Note that R^* and N^* should be inversely related to each other, and that correlation of R^* with β should be positive, while correlation of N^* with β should be negative. Note also that search rate and resource supply, which are unmeasured, can influence these relationships and the response of R^* and N^* to treatments.