

How Will Species Respond to Climate Change? Examining the Effects of Temperature and Population Density on an Herbivorous Insect

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ABSTRACT An important challenge facing ecologists is to understand how climate change may affect species performance and species interactions. However, predicting how changes in abiotic variables associated with climate change may affect species performance also depends on the biotic context, which can mediate species responses to climatic change. We conducted a 3-yr field experiment to determine how the herbivorous grasshopper *Camnula pellucida* (Scudder) responds to manipulations of temperature and population density. Grasshopper survival and fecundity decreased with density, indicating the importance of intraspecific competition. Female fecundity tended to increase with temperature, whereas grasshopper survival exhibited a unimodal response to temperature, with highest survival at intermediate temperatures. Grasshopper performance responses to temperature also depended on density. Peak survival in the low-density treatment occurred in warmer conditions than for the high-density treatment, indicating that the intensity of intraspecific competition varies with temperature. Our data show that changes to the temperature regimen can alter grasshopper performance and determine the intensity of intraspecific competition. However, the effects of temperature on grasshopper performance varied with density. Our data indicate the importance of the biotic context in mediating species responses to climatic factors associated with global change.

KEY WORDS temperature, grasshoppers, density dependence, intraspecific competition, metabolism

Many studies have shown potential effects of global climate change on individual species. For example, studies have found that increased temperature and/or elevated CO₂ concentrations can affect traits such as growth, survival, feeding rates, and phenology in insect herbivores (Hughes and Bazzaz 2001, Stiling et al. 2002, Veteli et al. 2002, Walther et al. 2002, Stiling et al. 2003, Williams et al. 2003, Abraham 2004). These changes may be indirect, caused by effects of environmental changes on plant foliar quality. For example, increased C:N ratios with elevated CO₂ concentrations lowers food quality and can lead to behavioral changes and/or decreased growth in insect herbivores (Roth and Lindroth 1995, Buse et al. 1998, Veteli et al. 2002). Alternatively, changes to species traits may result from direct effects of environmental changes on insect physiology, which may lead to altered resource intake. These direct and indirect effects of climate change on species traits may alter species interactions within a community. However, to predict how species interactions will be affected by climate change, it is important to first understand how individual species will respond to basic climate variables, such as tem-

perature. Next, it is important to understand how species' responses to climate variables might vary with population structure such as density, which varies considerably within and among years. This will provide a better understanding of how populations will respond to global climate change and a mechanistic basis on which to make predictions about species interactions in future climate scenarios.

Temperature is especially important for insects, influencing many physiological processes such as metabolism, digestion, phenology, behavior, and development (Heinrich 1993). Changes in temperature associated with global climate change may have impacts on insects at both the individual and population level. For example, temperature influences activity time and digestion rates, both of which determine resource intake for individuals (Heinrich 1993, Yang and Joern 1994b, Harrison and Fewell 1995). By influencing resource intake, temperature can affect both survivorship and fecundity.

Survivorship and fecundity may be affected by other factors such as population density (Varley et al. 1973, Belovsky and Slade 1995, Hopper et al. 1996, Agnew et al. 2002, Agrawal 2004, Hildrew et al. 2004), which arises from resource limitation as competitive pressure for food resources increases. Because tem-

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perature influences resource acquisition and density influences competitive pressure for resources, both factors may interact to determine population attributes such as survivorship and fecundity, as well as species interactions. Furthermore, because population density and temperature are not constant, it is important to measure the effects of these variables across a range of values and over time.

Grasshoppers provide a good model system for field studies examining the effects of density and temperature. First, the small body size of grasshoppers allows them to be easily manipulated in experimental enclosures (Joern and Klucas 1993, Ritchie and Tilman 1993, Schmitz 1994, Belovsky and Slade 1995). Second, the univoltine life history of many grasshoppers allows easy measurements of lifetime survival and fecundity within one season. Finally, many species of grasshoppers have been shown to exhibit density dependent survival and fecundity (Belovsky and Slade 1995, Laws 2004). Although there have been many laboratory studies on the effects of temperature on grasshoppers (Lactin and Johnson 1996, 1998; Uvarov 1977), few studies have manipulated thermal conditions in field experiments with grasshoppers (but see Chase 1996, Ritchie 1996).

We conducted a manipulative field experiment to examine the effects of abiotic conditions and population density on intraspecific competition in the herbivorous grasshopper, *Camnula pellucida* (Scudder) (Orthoptera: Acrididae). Abiotic conditions in the enclosures were manipulated with the use of removable plastic greenhouses or shade cloth. The combined effects of temperature and density on grasshopper performance traits (survival, fecundity, and body mass) were measured. This allows us to infer how temperature and population density might interact to affect intraspecific competition. By using a field study, we can allow grasshoppers to behaviorally thermoregulate and choose among food resources. Plant biomass and quality in response to greenhouse and shade cloth treatments were also measured to determine whether effects on grasshopper performance traits might be explained by changes to plant quality or abundance. This study will begin to show how climate-related factors (temperature) and population density might influence grasshopper responses to global climate change.

Materials and Methods

Study Site and Organisms. This research was conducted at the University of Notre Dame Environmental Research Center (UNDERC-East) in northern Wisconsin (46°14.53 N, 89°33.27 W). The study site is an old field that was clear-cut for dairy cattle ≈70 yr ago. The site is now dominated by grass, *Phleum pratense*, and the forbs, *Achillea millefolium*, *Solidago* spp., and *Asclepias speciosa*. Grasshoppers are the most abundant aboveground insect herbivore at the site, with *Camnula pellucida* (Scudder) and *Melanoplus dawsoni* (Scudder) (Orthoptera: Acrididae) being the two dominant grasshopper species. *C. pellucida*, the

species used in this experiment, is a univoltine, egg overwintering species that hatches over ≈2 wk in mid-June. *C. pellucida* preferentially consumes grasses but will occasionally eat forbs (Pfadt 1994). This species is often reported to be a pest species and experiences fluctuating population sizes capable of very high densities (Pfadt 1994).

Experimental Design. This experiment was conducted during the summers of 2002–2004. Grasshoppers were added to experimental enclosures (basal area: 0.5 m⁻²; height: 1 m) placed over natural vegetation. The enclosures were constructed of aluminum screen attached to a base of 7-cm-wide aluminum edging and buried at least 6 cm into the ground (see Belovsky and Slade 1995 for a complete description of enclosures). Enclosures were spaced at least 1.5 m apart, but we attempted to place enclosures over areas with similar vegetation.

Camnula pellucida nymphs (second and third instar) were collected with insect nets after hatching in mid-June. Nymphs were placed in terraria and fed ad libitum for at least 24 h to identify and prevent the use of injured individuals before stocking in enclosures. Grasshoppers were stocked in an even sex ratio at two densities (8 and 20 m⁻²) that reflect observed high and low field densities at our site. Additionally, some enclosures had no grasshoppers so that plant responses to temperature treatments could be examined (see below). Each enclosure was exposed to natural abiotic conditions (control) or temperature treatments that increased or decreased ambient temperature.

To manipulate temperature, removable greenhouses constructed of clear plastic sheeting (3.5 Mil thickness) were placed over the enclosures for 4, 6, and 8 h during each day in 2002. Because temperatures in the 8-h treatment became too hot for the grasshoppers, greenhouses were placed over the enclosures for 2, 4, and 6 h/d in 2003 and 2004. Alternatively, temperatures in enclosures were reduced by shading with 80% shade cloth for 4 and 6 h during each day. Including the control (ambient) enclosures, there were a total of six temperature treatments in each year. All treatments were set up by 0700 hours each morning, before the sun was high enough to shine on the enclosures over the surrounding forest. This schedule prevented the grasshoppers from basking and increasing their body temperatures before the shade cloths were set up. Treatments were randomly assigned to cages in each year and replicated four times. Enclosures without grasshoppers were replicated three times for each temperature treatment.

Temperature treatments may impact different aspects of the physical environment inside the enclosures such as humidity or air flow. However, the main effect of the greenhouse and shade cloth treatments was to alter ambient temperature inside the enclosures (see Results). Average temperature in the enclosures was measured hourly throughout the day with thermometers in enclosures ($N = 30$). Humidity was measured in the 6-h shade cloth, 6-h greenhouse, and control enclosures with a Hobotemp RH data

logger ($N = 46$). Ambient weather conditions at the site were measured with a Campbell Scientific weather station.

The temperature treatments shifted morning temperature relative to the control while allowing natural fluctuations in daily temperature to occur in experimental treatments. By providing for diurnal changes in ambient temperature, grasshoppers can shift activity to different parts of the day when ambient temperature is preferable. This approach may therefore provide a more realistic approximation of insect responses to climate change than laboratory studies in which temperature is generally held constant because it provides individuals the opportunity to behaviorally compensate for changes in temperature regimens.

Population Censuses. Once a week, the surviving grasshoppers in each enclosure were counted. The sex and developmental stage (nymph versus adult) for all grasshoppers in each enclosure were recorded. If all adult male grasshoppers in an enclosure died, one was added so that the females could be fertilized. These added males were not included in survival analyses.

In this experiment, as well as in previous experiments with grasshoppers at other sites, grasshopper densities in enclosures declined to a stable number that was maintained for up to 4 wk, after which the densities began to decline because of senescence and cold fall temperatures (Belovsky and Slade 1993, 1995; Chase and Belovsky 1994). Grasshopper survival was measured by dividing the number of grasshoppers in the enclosures at the stable density by the number of individuals stocked in the enclosures. The experiment was ended when grasshopper densities began to decline from this stable density in late season. All surviving grasshoppers were collected from the enclosures; females were frozen so that their reproductive tracts could be analyzed to estimate egg production (see below). Females were weighed in the laboratory to obtain frozen weights.

Fecundity was measured for females collected at the end of the experiment by examining reproductive tracts (Phipps 1949, Singh 1958, Lusi 1963, Lanois-Luong 1978, Bellinger and Pienkowski 1985, Sundberg et al. 2001). A grasshopper's reproductive tract consists of several ovarioles that produce eggs. Ovarioles that are currently forming an egg (functional ovarioles) can be counted to give a good approximation of current reproductive activity (Branson 2003). When an egg is successfully produced, the egg lining collapses to form a white or yellowish follicle resorption body at the base of the ovariole (Phipps 1949, Singh 1958, Bellinger and Pienkowski 1985, Sundberg et al. 2001). We used the number of functional ovarioles (current reproduction) plus the number of eggs produced (past reproduction) to measure fecundity for females. Fecundity was calculated for each female and averaged for each enclosure.

Plant Quality and Abundance. Plant quality and abundance were measured in each enclosure. Plant quality depends on nutrient content and how easily nutrients can be extracted (digested) by the herbivore. We measured chemical solubility; which is cor-

Table 1. Average, maximum, and minimum daytime temperatures ($^{\circ}\text{C}$) inside enclosures for each of the six temperature treatments

Temperature treatment	Average temperature \pm SD	Minimum temperature	Maximum temperature
6-h shade cloth	20.9 \pm 6.1	10.5	30.0
4-h shade cloth	20.5 \pm 5.9	10.0	30.5
Control	23.4 \pm 5.9	10.0	30.0
2-h greenhouse	22.6 \pm 5.8	11.0	30.0
4-h greenhouse	24.5 \pm 7.3	12.0	38.0
6-h greenhouse	26.4 \pm 7.7	12.0	41.0

related with *in vivo* digestibility for grasshoppers (Belovsky and Slade 1995) and plant nitrogen content for live vegetation collected from 0.1-m² plots in each enclosure at the end of the experiment in 2003 and 2004. Plants were sorted to grasses and forbs and dried at 60 $^{\circ}\text{C}$ for 24 h. Chemical solubility was measured in HCl and pepsin (Terry and Tilley 1964). Plant C:N ratios were measured with an elemental CHN analyzer (ECS 4010; Costech Analytical Instruments, Valencia, CA).

Total grass biomass was estimated from grass collected from 0.1-m² plots inside enclosures with no grasshoppers. By using cages without grasshoppers, we could isolate the effects of the temperature treatments on plant biomass from the effects of herbivory on plant biomass. Because *C. pellucida* preferentially feeds on grasses, analyses were run on grasses only.

Analyses. We used analysis of variance (ANOVA) to assess the effects of temperature treatment, grasshopper density, and year for each of our dependent variables: survival, fecundity, and female body mass. Year was treated independently because treatments were randomly assigned to enclosures each year of the experiment. Survival data were transformed using an arcsine transformation (Zar 1999). Statistics were performed with Systat v. 11 (SPSS 2000).

Results

Effects of Temperature Treatments on Temperature in Enclosures. Average ambient daytime temperature (0700–2000 hours) at the site varied among the 3 yr of the study. Ambient temperatures were lowest in 2004 (19.7 \pm 5.5 $^{\circ}\text{C}$ [SE]), intermediate in 2003 (21.1 \pm 4.7 $^{\circ}\text{C}$), and highest in 2002 (23.9 \pm 4.6 $^{\circ}\text{C}$). Greenhouse and shade cloth treatments altered ambient temperature in the enclosures while they were in place (Table 1; Fig. 1). Average daytime temperature in the control treatment was 23.4 $^{\circ}\text{C}$ (Table 1). While they were in place, shade cloth treatments decreased average daytime temperatures by \approx 3 $^{\circ}\text{C}$, whereas greenhouse treatments increased the average daytime temperature by up to 3 $^{\circ}\text{C}$ (Table 1; Fig. 1). Minimum daytime temperatures were lowest in the control and shade cloth treatments, whereas maximum temperatures were highest in the greenhouse treatments (Table 1).

Relative humidity did not vary significantly among temperature treatments ($F = 1.3$; $df = 5,785$; $P = 0.27$),

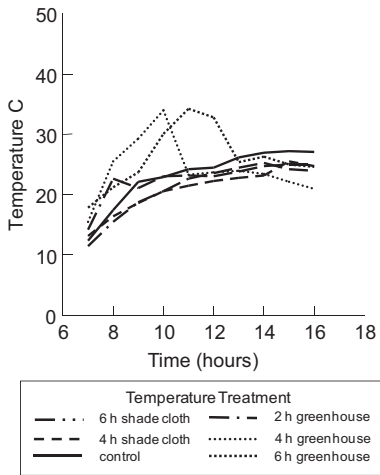


Fig. 1. Average temperature for each of the temperature treatments is plotted against time. Greenhouse treatments warm up faster and reach higher temperatures than control and shade cloth treatments.

although there was a trend for higher relative humidity in shade cloth treatments compared with control and greenhouse treatments (Fig. 2). Relative humidity did vary significantly over time of day ($F = 259.5$; $df = 1,785$; $P < 0.01$). The interaction term between temperature treatment and time of day was not significant ($F = 1.8$; $df = 5,785$; $P = 0.11$).

Survival. Final survival exhibited a unimodal response when plotted against temperature treatment, and high-density treatments elicited stronger responses (Fig. 3A). In 2002 and 2003, this unimodal response shifted with density, so that peak survival in the high-density treatment occurred in the control treatment, whereas peak survival for the low-density treatment occurred under the 4-h greenhouse treatment. In 2004, survival was again unimodal, but the peak survival occurred at the control treatment for both densities (Fig. 3A).

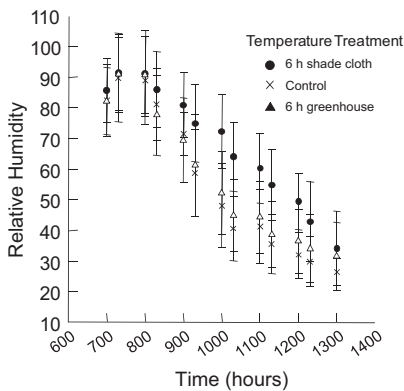


Fig. 2. Relative humidity is plotted against time for the control, 6-h greenhouse, and 6-h shade cloth treatments. Bars represent SD.

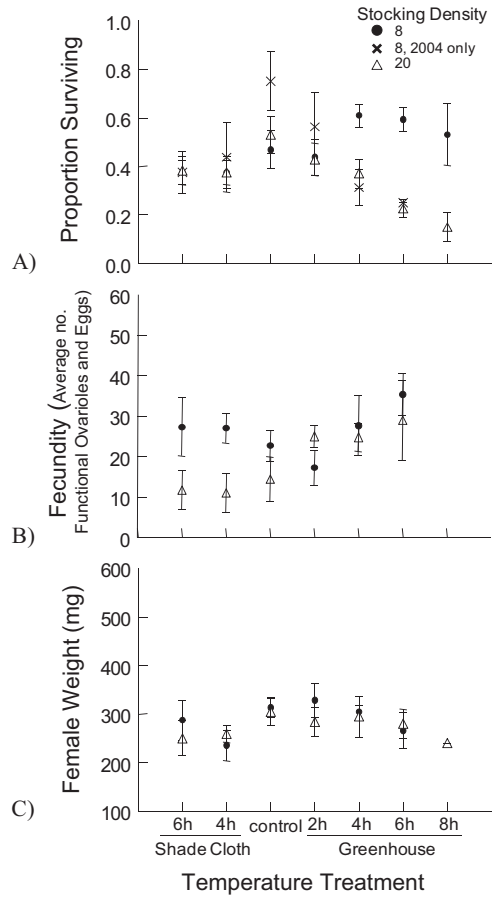


Fig. 3. Final proportion surviving (A), fecundity (B), and female body mass (C) are plotted against temperature treatment for each density. Bars represent SE.

Survival varied significantly with temperature treatment and density ($F = 2.63$; $df = 6,129$; $P = 0.02$ and $F = 11.82$; $df = 2,129$; $P < 0.001$, respectively), but effect of year on survival was not significant ($F = 1.81$; $df = 2,129$; $P = 0.17$).

Fecundity. Fecundity generally increased with temperature treatments, but this trend was stronger in the high-density treatment (Fig. 3B). The effect of year was not significant ($F = 0.1$; $df = 1,48$; $P = 0.74$), so years were pooled. The effects of density on fecundity were significant ($F = 5.6$; $df = 1,44$; $P = 0.02$), but temperature treatment and the interaction term were not significant ($F = 2.0$; $df = 5,44$; $P = 0.09$ and $F = 1.8$; $df = 5,44$; $P = 0.13$, respectively).

Body Mass. Body mass of females collected at the end of the experiment exhibited a weak unimodal trend with temperature treatment (Fig. 3C), although there was no significant effect of temperature treatment ($F = 0.99$; $df = 6,70$; $P = 0.44$). Body mass of *C. pellucida* did not differ significantly between densities ($F = 0.9$; $df = 1,70$; $P = 0.34$) but did differ significantly among years ($F = 3.7$; $df = 2,70$; $P = 0.03$), with body mass in 2002 lower than in 2003 and 2004 ($F = 5.29$; $df = 2,70$; $P = 0.01$).

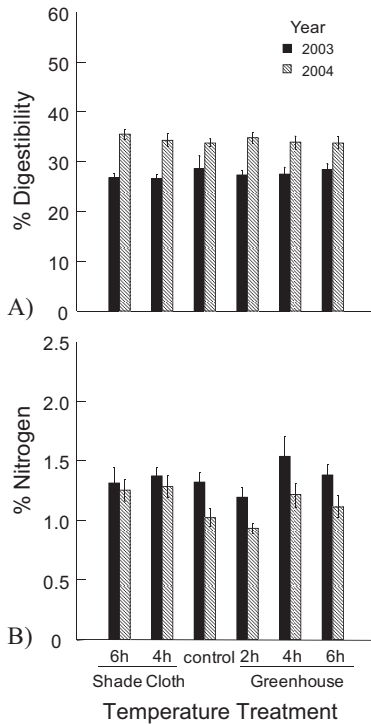


Fig. 4. Chemical solubility (A) and percent nitrogen content (B) are plotted for each temperature treatment. Bars represent SE.

Vegetation Quality and Abundance. There was no significant difference in chemical solubility of grasses among temperature treatments ($F = 0.1$; $df = 5, 120$; $P = 0.98$; Fig. 4A). However, chemical solubility did vary significantly between years, with higher digestibility in 2004 than 2003 ($F = 90.9$; $df = 1, 120$; $P < 0.01$; Fig. 4A). Nitrogen content of grasses did vary significantly between years, with higher nitrogen content in 2003 than 2004 ($F = 20.9$; $df = 1, 120$; $P < 0.01$; Fig. 4B). Nitrogen content varied significantly with temperature treatment ($F = 2.9$; $df = 5, 120$; $P = 0.02$; Fig. 4B) because of lower nitrogen content in the 2-h greenhouse treatment. Biomass of grasses in the one-trophic-level treatments did not vary significantly by year or temperature treatment ($F = 1.6$; $df = 1, 29$; $P = 0.22$ and $F = 1.3$; $df = 5, 29$; $P = 0.30$, respectively).

Discussion

The shade cloth and greenhouse treatments altered ambient temperature relative to the control treatment while they were in place. Ambient morning temperatures inside the greenhouse treatments reached 19°C, the ambient temperature required for *C. pellucida* to begin feeding and digesting (Parker 1930, Hewitt and Onsager 1982, Pfadt 1994), about 1 h earlier than in the control treatments, and about 2 h earlier than in the shade cloth treatments (Fig. 1). By altering the time of day when grasshoppers can potentially begin feeding,

the temperature treatments influence grasshopper resource acquisition and grasshopper performance.

Temperature treatments had the strongest effect on grasshopper survival, which exhibited a unimodal relationship with temperature treatment at both low and high densities. We propose two hypotheses to explain this relationship. First, the temperature treatments may have altered plant quality or plant abundance, indirectly affecting grasshopper survival through altered nutrient acquisition. Second, grasshopper survival in each of the temperature treatments may depend on how temperature affects net resource intake.

Effects of Temperature Treatments on Plant Quality and Abundance. Grasshopper performance declines as plant abundance and/or plant quality decreases (Joern and Behmer 1997, 1998; Danner and Joern 2003; Jonas and Joern 2008). However, in our study, grass biomass did not vary significantly among temperature treatments or between years and cannot explain patterns of grasshopper survival. Grass chemical solubility also did not vary with temperature treatment in either year that vegetation was collected. Nitrogen content of grasses did vary significantly with temperature treatment. However, this was only caused by a decrease in nitrogen content in the 2-h greenhouse treatment, a result that would not explain the observed unimodal response of grasshopper survival. This suggests that the response of *C. pellucida* to the temperature treatments was not driven by indirect effects of the temperature treatments on plant quality or plant abundance.

Temperature Effects on Net Resource Intake. Observed patterns in grasshopper survival may be caused by the effects of temperature treatments on physiological processes affecting net resource intake, which is determined by resource intake (digestion and feeding) relative to metabolism (i.e., energetic requirements). Temperature differently affects these physiological processes: metabolism increases exponentially with temperature (Gillooly et al. 2001, Clarke and Fraser 2004), whereas intake increases linearly with temperature (Harrison and Fewell 1995). Performance is determined by how much resource intake exceeds resource requirements. This hypothesis can explain the unimodal relationship observed between survival and temperature treatment if altered temperatures in the shade cloth and greenhouse treatments reduce net resource intake relative to the control treatments.

Although both metabolism and resource intake are reduced by decreased temperatures in shade cloth treatments, cooler morning temperatures may delay the onset of feeding behavior and thus resource intake relative to control and greenhouse treatments. Reduced temperatures in the shade cloth treatments would also slow feeding and digestion rates, further reducing resource intake relative to metabolism. This would cause reduced grasshopper performance in shade cloth treatments relative to control treatments.

In the greenhouse treatments, warmer temperatures increase grasshopper resource intake in three ways. First, warmer temperatures increase grasshopper

per feeding and digestion (Uvarov 1977, Cammell and Knight 1992, Hughes 2000), in part by decreasing food residence time (Yang and Joern 1994b), enabling increased resource acquisition (Yang and Joern 1994a). Second, increased digestive efficiency enables grasshoppers to consume poorer-quality food that may be unavailable at lower temperatures (Heinrich 1993, Yang and Joern 1994b, Harrison and Fewell 1995), thus widening the resource pool. Third, the greenhouse treatments may increase resource intake by raising morning temperatures so that grasshoppers can begin feeding earlier in the day than in control and shade cloth treatments. However, resource requirements increase exponentially with temperature as metabolic costs rise, serving to reduce net resource intake, especially in the warmest treatments. Furthermore, at high temperatures, physiological stress may force grasshoppers to reduce activity, further reducing intake relative to requirements and leading to lower performance in greenhouse treatments relative to control treatments.

The effects of temperature on net resource intake can also explain why peak grasshopper survival occurred at different temperature treatments for low and high densities. Warmed temperatures in the greenhouse treatments would increase metabolism, leading to higher per capita resource requirements and intensified competitive pressure. Population density, which determines per capita resource availability, further determines competitive pressure. Therefore, competition should be more intense in the high-density greenhouse treatments than in the low-density greenhouse treatments. This would explain why peak survival occurs in cooler treatments for high-density populations than for low-density populations (control treatment versus 4-h greenhouse treatment; Fig. 3A).

Density Dependence. Grasshoppers often compete exploitatively for food resources (Ritchie and Tilman 1992, 1993; Joern and Klucas 1993; Schmitz 1994; Belovsky and Slade 1995; Belovsky and Slade 2000), which can lead to density dependent performance (Belovsky and Slade 1995; Ritchie 1996, 2000). Therefore, it is not surprising that both fecundity and survival exhibited density dependence. However, it is interesting that the expression of density dependence also varied with temperature treatment. For example, fecundity exhibited density dependence only in the shade cloth treatments, whereas survival exhibited density dependence only in the greenhouse treatments.

Our data show that population density can modify the effects of temperature on grasshopper performance traits. Variation in density dependence with temperature was also observed by Ritchie (2000) in a similar study with the grasshopper *M. sanguinipes* (Fabricius) (Orthoptera: Acrididae). Our experiment, along with these other studies, highlights the importance of examining potential effects of global climate change on populations across a range of densities. Because density can alter species responses to temperature change, predictions of species responses to global climate change based on measurements of performance taken at only one population density

may not be adequate. This will be particularly important for populations in which density varies widely among years, such as for herbivorous insects like *C. pellucida* (Reigert 1967, Uvarov 1977).

Trade-Offs. Despite differences in temperature and competitive pressure among temperature treatments and between densities, all surviving females reached a similar body mass within years. We do not know the body mass of individuals that died during the experiment, which may have been smaller. Because female body mass did not vary among temperature treatments, one explanation is a size threshold that *C. pellucida* must reach to be competitive, but more work is needed to test this hypothesis.

In a study on the effects of temperature on digestive capabilities of *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae), Yang and Joern (1994b) discovered that temperature only affected weight gain at very low nutritional food quality (1% N), but not at medium (3% N) and high nutritional quality (5% N). They argued that at high- and medium-quality diets, *M. differentialis* was able to compensate for temperature changes by regulating digestion rate (e.g., gut size, food residence time). The average nitrogen content for vegetation in this study was 1.2% for grasses and 1.5% for forbs. It is possible that vegetation quality was high enough for *C. pellucida* that weight gain (and therefore body mass) was not affected by the range of temperatures encountered in this study. This may also represent a trade-off in resource allocation to growth, survivorship, and fecundity. Grasshoppers may have chosen to allocate more resources to survival and fecundity rather than growth, after reaching some threshold body size.

In the high-density greenhouse treatments, fecundity tended to increase while survivorship decreased, indicating that, in the high-density greenhouse treatments, grasshoppers allocated more resources to fecundity than survivorship. Trade-offs like these may be more important under warmer conditions if intraspecific competition intensifies with temperature, as in this study.

How Will *C. pellucida* Respond to Climate Change? The treatments used in this experiment manipulated temperatures relative to ambient in the morning and early daytime. Although this does not simulate future weather patterns projected with climate change, we believe some predictions about grasshopper responses to climate change may be inferred from our data. Average daytime summer temperatures in the Great Lakes region where our study site is located are projected to increase at least 3–5°C by 2099 (Kling et al. 2003), which is similar to increases in temperature caused by the greenhouse treatments used in this study. Along with changes in mean temperature, global climate change models also project an increase in the variance of climatological variables (Easterling et al. 2000, Houghton et al. 2001, Houghton 2004). Grasshopper survival in the control treatments was similar among years, although average daytime temperature varied, indicating that grasshoppers acclimated to differences in average temperature among

years. However, deviations from mean temperature within years, as caused by the shade cloth and greenhouse treatments, did lead to changes in grasshopper performance. This suggests that short-term fluctuations in climatological variables, which are expected with climate change (Easterling et al. 2000, Houghton et al. 2001, Houghton 2004), may have more negative effects on populations of *C. pellucida* than long-term shifts in mean temperature alone.

Our results also indicated that increases in temperature can have negative effects on grasshopper survival, especially at high grasshopper densities. This reduction in survival with temperature occurred even though the temperature treatments did not alter abundance or quality of grasses. The observed decrease in grasshopper performance with increased temperature runs counter to many studies of insect responses to climate change, which suggests that insect performance (e.g., growth and development rates) may be enhanced by increasing temperatures (Bale et al. 2002, Zvereva and Kozlov 2006, Dermody et al. 2008, O'Neill et al. 2008). We show that that temperature changes associated with global climate change may also have negative impacts on insect populations, especially at higher densities. Finally, our data indicate the need to evaluate species responses to climate change over a range of population densities, because density can alter species responses to abiotic variables.

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