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## Resource-mediated impact of spider predation risk on performance in the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae)

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**Abstract** In response to increased exposure to predators when searching for food, many prey increase the frequency of antipredator behaviors, potentially reducing foraging rate and food intake. Such direct, nonlethal interactions between predators and prey resulting in reduced food intake can indirectly influence lifecycle development through effects on growth, developmental rate, and survival. We investigated the general hypothesis that individual performance of a herbivorous insect can be negatively affected when exposed to nonlethal predation risk, and that the response can be mediated by food quality. This hypothesis was tested using the common rangeland grasshopper *Ageneotettix deorum* with and without exposure to common wolf spider predators (Lycosidae, *Schizocosa* spp.) on both untreated natural and fertilized vegetation. All spiders were rendered temporarily incapable of direct feeding by restricting function of the chelicerae with beeswax. Detectable responses by grasshoppers to spiders indicate indirect consequences for lifecycle development. Grasshopper performance was measured as hind femur growth, duration of nymphal lifecycle stages, and survivorship in a caged field experiment conducted over 2 years. Grasshoppers developed faster and grew 3–5% larger when allowed to forage on fertilized vegetation in the absence of risk from a spider predator. Failure-time analysis illustrated enhanced survival probability in response to elevated food quality and the negative effects of grasshopper susceptibility to nonlethal predation risk. Performance on food of relatively low, ambient quality with no predation risk equaled that of grasshoppers caged with high quality vegetation in the presence of a modified spider. Increased resource quality can clearly moderate the negative life history responses caused by the behav-

ioral modification of grasshoppers when exposed to spider predation risk, a compensatory response.

**Keywords** Compensatory responses · Nonlethal interactions · Grasshopper ecology · Lycosid wolf spider predation · Nebraska Sandhills grassland

### Introduction

Indirect consequences of predation on age and size at maturity of prey in response to release from competition for food or altered foraging efficiency can be significant (Abrams and Rowe 1996). Prey often balance food acquisition against risk to predation by altering foraging behavior and reducing feeding levels (Lima and Dill 1990; Lima 1998a, 1998b; Abrams and Schmitz 1999), with important consequences for life history attributes (Skelly and Werner 1990; Lima 1998a, 1998b; McPeck and Peckarsky 1998; Peckarsky et al. 2001). In such nonlethal encounters with predators, prey can be less active (Werner 1992; Peacor and Werner 2000), consume less food (Peckarsky et al. 1993; Stamp and Bowers 1993), or use different habitats while foraging (Holbrook and Schmitt 1988; Rothley et al. 1997; Ovadia and Schmitz 2002). In turn, these prey responses can result in reduced growth and developmental rates, increased mortality from starvation, or decreased fecundity (Semlitsch 1987; Skelly and Werner 1990; Stamp and Bowers 1991, 1993; Skelly 1992; Peckarsky et al. 1993, 2001; Werner and Anholt 1993, 1996; Scrimgeour and Culp 1994; Lima 1998a, 1998b; McPeck and Peckarsky 1998; Peckarsky and McIntosh 1998; Nakaoka 2000; Peacor and Werner 2000). Clearly, nonlethal encounters by prey with predators can substantially influence key life history attributes.

While nonlethal interactions may alter foraging behavior, elevated food quality may modify consumer performance in a compensatory fashion. Most herbivores forage in a heterogeneous nutritional landscape in which host plant quality typically varies in space and time, especially as the season progresses (Denno and McClure

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1983; Bernays and Chapman 1994). Often, unpredictable events can affect plant quality locally, including prior feeding on a plant (Jones and Coleman 1991; Alward and Joern 1993; Redak and Capinera 1994; Karban and Baldwin 1997), small-scale spatial variation in plant-water relationships (Gershenson 1984; Bokhari and Trent 1985; Chapin et al. 1987; Louda and Collinge 1992; White 1993), or transient effects such as nutrient import by urination from large ungulates passing through an area (Hartnett et al. 1997; Coppedge and Shaw 1998). Costs of nonlethal predation risk resulting from less total food eaten might be overcome to some degree if consumers compensate for reduced food intake by eating higher quality food (Loader and Damman 1991; Oedekoven and Joern 2000).

In grasshoppers, successful performance during immature stages of the lifecycle requires sufficient food, the bulk amount dependent primarily upon nutritional intake (Heidorn and Joern 1987; Joern and Alward 1988; Yang and Joern 1994; Simpson et al. 1995; Joern and Behmer 1998; Raubenheimer and Simpson 1999). Assuming that high quality plant material exists, grasshoppers should search for and consume resources that will maximize growth, survival, and reproduction (Joern et al. 1986; Joern and Gaines 1990; Hinks et al. 1993; Belovsky et al. 1996). Predation risk compromises this goal, however, as the best plant tissues are often situated such that susceptibility to predators while foraging is increased (Joern and Rudd 1982; Beckerman et al. 1997; Schmitz et al. 1997; Oedekoven and Joern 2000; Ovadia and Schmitz 2002). Size-selective spider predation negatively impacts immature grasshopper performance (Oedekoven and Joern 1998; Okuyama 1999) possibly by modifying feeding and defensive behaviors, resulting in reduced foraging efficiency (Wootton 1994; Beckerman et al. 1997; Schmitz et al. 1997; Schmitz 1998; Danner and Joern 2003).

Spider predation risk can alter grasshopper activity budgets (Rothley et al. 1997; Schmitz et al. 1997; Danner and Joern 2003), specifically causing reduced access to high quality food resources as a result of increased defensive activity. Given that spiders are able to modify the ability of grasshoppers to obtain sufficient high quality food, important life history characteristics of the grasshoppers that require these resources may also be affected. We hypothesize that nymphal development, growth, and survivorship is negatively affected because of altered foraging activity caused by the presence of spiders (Schmitz 1998; Danner and Joern 2003). Eating high quality food may counteract the anticipated reduction in performance resulting from predation risk, suggesting that the interaction between grasshoppers and their spider predators may be mediated by elevated resource quality (Oedekoven and Joern 2000): when ambient food quality is higher, less time is required to find sufficiently nutritious food and exposure to predation risk is subsequently reduced, or individuals obtain sufficient nutrition when forced to forage in a shorter time period.

Using field experiments in the Nebraska Sandhills grassland, we examined how enhanced food quality and increased perception of spider predation risk combined to influence growth, development, and survival of immature *Ageneotettix deorum* (Scudder), a common rangeland grasshopper found throughout much of west central North America. Based on known dietary requirements (Yang and Joern 1994; Joern and Behmer 1998; Oedekoven and Joern 1998, 2000) and susceptibility of grasshoppers to predation risk from lycosid spiders (Beckerman et al. 1997; Schmitz et al. 1997; Oedekoven and Joern 1998, 2000; Schmitz 1998; Okuyama 1999), we hypothesized that immature *A. deorum* would respond positively to fertilized plant material and negatively to the risk of spider predation. Given prior evidence of compensatory interactions between resource quality and predator avoidance (Price et al. 1980; Beckerman et al. 1997; Oedekoven and Joern 2000), we also investigated the effects that combinations of these treatments had on performance responses. Specifically, we predicted that:

1. Spider predation risk negatively affects grasshopper survivorship, increases the time needed to complete development, and decreases growth as a result of altered behavior during nymphal stages when susceptibility to predation risk is high.
2. Readily available, nutritionally high-quality food compensates for the negative effects of spider predation risk, such that no difference in grasshopper performance will be detected between treatments without predation risk and ambient resource quality versus a spider present while higher quality food is available.
3. Predation risk and resource quality treatments act synergistically to affect grasshopper growth and development; so that treatment combinations of 'high food quality and no predation risk' are expected to maximize grasshopper performance, while 'low resource quality coupled with spider predation risk' will prolong development and retard growth.

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## Materials and methods

### Study site

We conducted field experiments during the summers of 2001 and 2002 at Arapaho Prairie, a site located in the Nebraska Sandhills grasslands (Arthur County). This site is situated on sandy soils with a highly variable topography composed of steep slopes, ridges and flat valleys, and is represented by plant species characteristic of both short and tall grass prairie with an open vegetation structure, including much bare ground (Joern 1985). Approximately 200 plant species are found, of which 80% are forbs; roughly 80% of the biomass and structure of vegetation are contributed by grasses (Keeler et al. 1980; Barnes and Harrison 1982). Sandy soils at Arapaho Prairie are nutrient poor, and addition of nitrogen fertilizer readily increases plant production and enhances foliar quality (Joern and Alward 1988; Oedekoven and Joern 1998, 2000).

*Ageneotettix deorum* is generally one of the most abundant of approximately 30 grasshopper species that occur regularly at the site and is graminivorous, primarily preferring grama grass species

in the genus *Bouteloua* (Joern 1985). Average adult density of all grasshopper species frequently approaches 4–5 adults/m<sup>2</sup> (Joern 1982), with *A. deorum* averaging 1–2 adults/m<sup>2</sup> (Joern, unpublished data); immature *A. deorum* density reached 30 individuals/m<sup>2</sup> in some habitats during this study (Danner 2002).

Numerous predators of grasshoppers reside in this system, including spiders, robberflies, various tachinid and sarcophagid parasitoids, mites, solitary wasps, and birds (primarily grasshopper sparrows and western meadowlarks) (Joern and Rudd 1982; Joern 1988, 1992; Oedekoven and Joern 1998, 2000). Birds tend to feed on larger adult grasshoppers (Joern and Gaines 1990; Joern 1992), while immature grasshoppers are susceptible to spider and insect predation, especially from lycosid wolf spider species (*Schizocosa* spp. at this site) (Oedekoven and Joern 1998, 2000). All wolf spiders used as predators in this experiment were caught on site using pitfall traps and by hand in chance encounters. All grasshopper nymphs used were collected from Arapaho Prairie and surrounding areas using sweep nets.

Weather at this site is highly variable among years. Based on data collected since 1987 from an on-site weather station, the mean ( $\pm 1$  SE) annual precipitation is 37.3 $\pm$ 6.1 cm. Normal precipitation between 1 June and 15 August is 14.9 $\pm$ 1.7 cm. In 2001, rainfall during this period was 17.2 cm. In 2002, only 11.6 cm of rain fell over this time period, with 52% of the precipitation falling during a 12-h period the first week of July.

### Cage design

We used field cages (0.33 m wide $\times$ 0.33 m deep $\times$ 0.80 m tall; 0.10 m<sup>2</sup> basal area), similar to those described by Oedekoven and Joern (1998), buried 20 cm into the ground over suitable vegetation to confine experimental grasshoppers. After clearing the area of spiders, cages were placed over natural vegetation that included at least 50% cover of blue grama grass (*Bouteloua gracilis*), the primary host plant of *A. deorum*. Vegetation structure was low (<10 cm average height) at the beginning of the experiment and reached heights up to 50 cm in some cages by the end in mid-August: open areas of low structure were available in all cages at all times. All four sides and lids of the cage were covered with insect screening with a mesh size of less than 1 mm, successfully retaining experimental grasshoppers and spiders while preventing the entry of other grasshoppers and predators. Cages were positioned 1.0–1.5 m apart on all sides. We stocked 72 cages in 2001 and 120 cages in 2002. With four combinations of treatments, we replicated treatments 18 times in 2001 and 30 times in 2002 in a randomized complete block design.

### Experimental conditions

Predator risk and food quality were manipulated in a 2 $\times$ 2 factorial treatment design allocated randomly within blocks. A randomized complete block experimental design was used for two reasons:

1. Blocking minimized unknown differences in plant community composition or ambient foliar quality of food plants associated with microtopographic relief and subtle differences in soil in this dune-based grassland.
2. Additionally, all cages in a block were stocked on the same day, but a sufficient number of grasshoppers could not be collected, sorted, and prepared to stock all cages in the experiment on the same day without undue stress to the grasshoppers. Blocking accounted for unknown effects resulting from the necessity that different blocks were stocked on different days; two blocks were stocked per day when possible.

Different levels of food quality were established by applying an aqueous solution of Miracle Gro (Sterns, Port Washington, N. Y.) N-P-K (15-30-15) plant fertilizer at a concentration of 7.5 g N/m<sup>2</sup> to randomly selected cages in each block. Remaining cages were treated with an equivalent amount of water only, and represent

ambient, low food quality conditions. A 230 cm<sup>2</sup> sample of aboveground biomass (approximately 20% of cage biomass) from each of 40 randomly selected cages (20 within each level of food quality treatment) was clipped, dried, and weighed both prior to and after the experiment in order to assess the effect of fertilizer on plant nitrogen content. Cages were stocked with seven immature grasshoppers, a level about twice the average natural field densities at the time, but within the range found at some sites (Danner 2002). Field-collected grasshoppers were arbitrarily assigned to experimental cages.

For the predation risk treatment, half of the cages were stocked with one wolf spider rendered nonlethal by applying beeswax to the chelicerae as described by Schmitz et al. (1997) and Okuyama (1999). Following experimental trials, the wax was removed so spiders could feed and no mortality was observed. The application of this treatment removes the threat of direct predation while simultaneously retaining any indirect effects resulting from altered prey behavior in response to spider presence (Schmitz et al. 1997; Okuyama 1999; Danner and Joern 2003).

### Grasshopper performance

Survival, developmental stage and growth were recorded over the experiment's duration for all grasshoppers. In 2001, cages were arbitrarily stocked with early fourth-instar nymphs and developmental rate was estimated as the length of time required for survivors to complete two molts. In 2002, we stocked cages with early third-instar nymphs and calculated developmental rate as the time required to complete three immature lifecycle stages. Developmental stage of immature grasshoppers was based on wing pad development (Scoggan and Brusven 1972). The length of the right hind femur was used to measure individual growth. Femur length adequately approximates grasshopper size (Cueva del Castillo et al. 1999), and is readily measured in the field. All grasshoppers within a cage were measured at each sampling period in order to obtain the most reliable estimate of growth over time. Survival was tracked by censusing every 2–4 days over the experiment's duration. In 2001, all surviving grasshoppers had completed pre-reproductive development after approximately 18 days. The experiment continued for approximately one more week at which time both grasshoppers and spiders were released. Although an additional life stage was followed during the 2002 season, the same protocols were followed.

### Statistical analyses

Differences in growth and development rate were assessed with ANCOVA using the average for all grasshoppers within each cage as the experimental unit (Sokal and Rohlf 1981). Cage density was used as a covariate to account for the potentially negative effects of density dependence. Growth based on hind femur length was analyzed using repeated-measures ANCOVA with the proportion surviving to complete the final molt as a covariate. All specific treatment contrasts were analyzed using Tukey's adjustment to avoid increasing Type I errors given the large number of planned comparisons (Kuehl 2000). Variances among treatments for developmental rate were homogeneous. Femur growth data were log-transformed to meet the assumption of equal variance. Tests for homogeneous slopes in ANCOVA were conducted (SAS Online Doc, V8), resulting in non-significant differences ( $P > 0.45$ ). Survival trajectories of resource quality and predation risk treatments were assessed using life table techniques and failure time analysis (Fox 2001). Analyses of developmental rate and growth were performed using Proc GLM in SAS/STAT. Survival data were analyzed using Proc LIFETEST in SAS/STAT. Survivorship curves were compared using a Wilcoxon rank test coupled with subsequent alpha-corrected multiple comparisons to determine specific differences between treatment combinations. Because of variation in weather patterns between years, analyses for 2001 and 2002 were

conducted separately. Results are presented in their non-transformed state.

## Results

### Resource quality

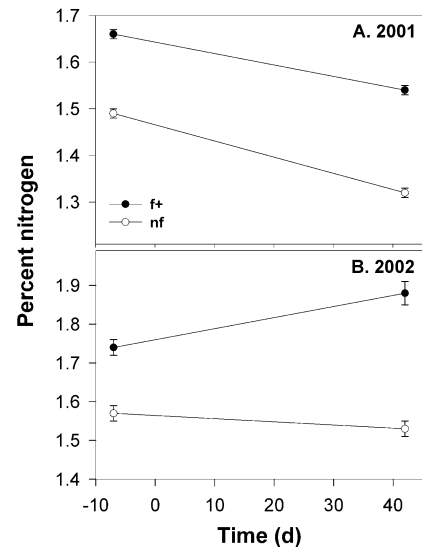
Nitrogen content of vegetation from cages is shown in Fig. 1. In both years there was a significant increase in foliar nitrogen content in the fertilizer treatment relative to ambient controls (2001  $F_{1,38}=6.77$ ,  $P=0.01$ ; 2002  $F_{1,38}=6.30$ ,  $P=0.02$ ). In 2001, nitrogen content for both treatments decreased over the growing season (Fig. 1), but did not change significantly in 2002 ( $F_{1,38}=1.67$ ,  $P=0.20$  in fertilized cages;  $F_{1,38}=0.20$ ,  $P=0.66$  in watered cages) (Fig. 1). Levels of nitrogen content of plant samples were well within typical levels, and possibly a bit lower than normal (Oedekoven and Joern 2000).

### Survivorship

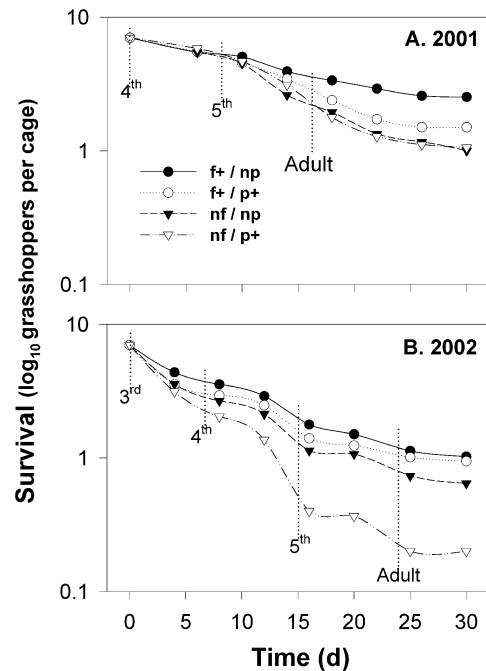
Differences were detected between survival trajectories of grasshoppers among the various treatment combinations in both years (Fig. 2). In 2001, grasshoppers in cages that combined no predation risk and high resource quality showed a significantly greater probability of survival than other treatment combinations; approximately 36.5% (25 grasshoppers/m<sup>2</sup>) of the original cohort survived compared to a mean survival of 19.4% (14 grasshoppers/m<sup>2</sup>) for the other three treatments combined. The effect of food nutritional content on survivorship was highly significant ( $\chi^2=14.62$ ,  $P<0.01$ ), while predation risk evaluated over all treatments (Fig. 2) did not significantly affect survivorship ( $\chi^2=0.08$ ,  $P=0.11$ ). In 2002, a drier year, survivorship distributions (Fig. 2) were significantly affected by both predation risk ( $\chi^2=15.97$ ,  $P<0.01$ ) and resource quality ( $\chi^2=34.82$ ,  $P<0.01$ ). By the end of the experiment, approximately 11% survival (7.7 grasshoppers/m<sup>2</sup>) was observed, except under treatment conditions of low quality food coupled with high predation risk, where only 3% (2.1 grasshoppers/m<sup>2</sup>) of the grasshoppers survived ( $Z=5.29$ ,  $P<0.01$ ) (Fig. 2).

### Developmental rate and growth

Increased host nutritional quality and absence of spider predation risk both resulted in a significantly increased rate of nymphal development of grasshoppers in both 2001 ( $F_{9,62}=3.15$ ,  $P<0.01$ ) and 2002 ( $F_{13,106}=3.67$ ,  $P=0.01$ ) (Table 1; Fig. 3). In 2001, grasshoppers completed two instars approximately 12.5% faster when food plants were fertilized. In 2002, development was approximately 7.0% faster to complete three nymphal instars. Similar accelerated development was observed between the predation risk treatments (Fig. 3). Results were consistent between years regardless of differences in



**Fig. 1A, B** Nitrogen concentration (mean $\pm$ 1 SE) of aboveground biomass clippings ( $n=20$  per food quality treatment per date) sampled prior to and after the experiment ( $F+$  fertilizer addition,  $NF$  no fertilizer). The same treatment applications were used for both years. Differences in dynamics are due to uncontrollable yearly effects, most probably severe drought conditions in 2002. In 2001, a fertilizer treatment was applied during the third week of June, and in 2002 fertilizer was applied during the first week of June



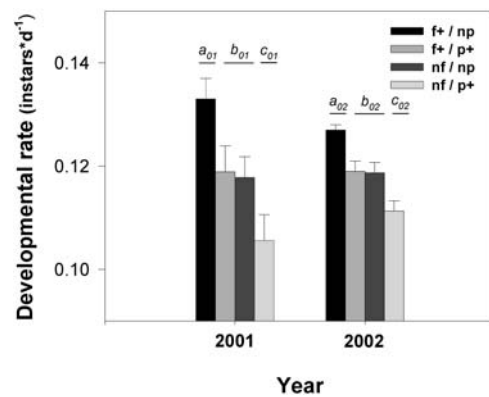
**Fig. 2A, B** Survival trajectories of grasshoppers (mean $\pm$ 1 SE) for fertilizer ( $F+$  fertilizer addition,  $NF$  no fertilizer) and predation risk ( $P+$  predator addition,  $NP$  no predator) treatment combinations using PROC Lifetest in SAS. Dotted lines represent median developmental lifecycle stage, calculated over all treatment groups

**Table 1** Type III ANOVA for the mean duration of immature development of grasshoppers that survived to become adults in experimental cages. Years were analyzed separately because of the differences between experimental protocols employed. The number of grasshoppers per cage at the time of the final molt was used as a covariate

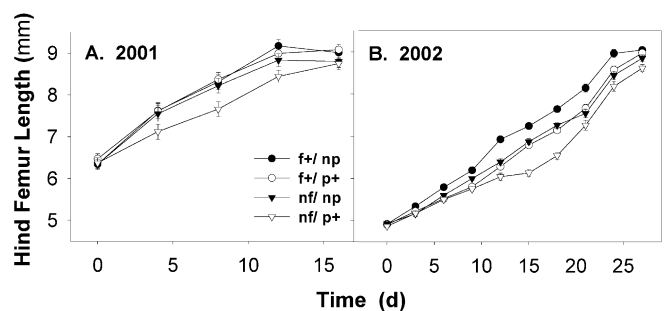
Source	df	MS	F	P
2001				
Block (B)	5	5.93	0.59	0.7113
Fertilizer (F)	1	63.33	6.25	0.0160
Predation (P)	1	46.03	4.54	0.0384
F×P	1	1.98	0.20	0.6603
B×F	5	5.54	0.55	0.7402
B×P	5	1.98	0.20	0.9629
B×F×P	5	10.28	23.49	0.0582
Survivors/cage	1	0.26	0.03	0.8724
Error	47	10.14		
2002				
Block (B)	9	3.38	1.19	0.3100
Fertilizer (F)	1	35.73	12.57	0.0007
Predation (P)	1	26.58	9.35	0.0030
F×P	1	3.37	1.19	0.2796
B×F	9	1.56	0.55	0.8356
B×P	9	4.11	1.44	0.1837
B×F×P	9	2.57	0.9	0.5269
Survivors/cage	1	0.01	0.01	0.9750
Error	79	2.84		

the number of developmental stages followed. Assessment of the role of the resource quality treatment under predator risk conditions revealed a 12.2% increase in developmental rate in 2001 ( $t=2.03$ ,  $P<0.05$ ) and a 7.2% increase in 2002 ( $t=3.14$ ,  $P<0.01$ ) when vegetation was fertilized in comparison to watered controls (Fig. 3).

In both years of the experiment, increased resource quality significantly enhanced the growth of immature grasshoppers (repeated-measures, between subjects ANCOVA, 2001  $F_{1,62}=4.72$ ,  $P=0.03$ ; 2002  $F_{1,106}=63.50$ ,  $P<0.01$ ; Fig. 4). Hind femurs of adults from fertilized treatments were approximately 3.3% longer than those growing on lower quality food after completion of development in 2001 and 3.1% longer in 2002. In 2001, predation risk did not significantly affect femur growth ( $F_{1,62}=1.25$ ,  $P=0.27$ ). In 2002, however, threat of predation did significantly reduce growth ( $F_{1,106}=78.48$ ,  $P<0.01$ ). The combination of no predation risk and high resource quality in 2002 resulted in a significant 5.0% increase in final size in comparison to predation risk coupled with low food quality ( $t=3.66$ ,  $P<0.01$ ; Fig. 4). Comparisons between no predation threat coupled with low quality food versus predation risk and high food quality treatments were never significantly different, over the entire sampling interval (Fig. 4). Under predator risk conditions, final size of grasshoppers was approximately 3.8% larger in 2001 ( $t=1.60$ ,  $P=0.11$ ) and 4.2% larger in 2002 ( $t=3.09$ ,  $P<0.01$ ) when vegetation was enhanced with the fertilizer treatment (Fig. 4).



**Fig. 3** Average developmental rate of caged grasshopper populations that survived to adulthood (mean±1 SE). Trends are consistent even though only two stages were followed in 2001, while three stages were observed in 2002. Significant differences in Tukey-adjusted multiple comparisons ( $\alpha=0.05$ ) are denoted by different letters above the bars



**Fig. 4A, B** Growth trajectory of the hind femur of grasshoppers (mean±1 SE) for fertilizer (F+ fertilizer addition, NF no fertilizer) and predation-risk (P+ predator addition, NP no predator) treatment combinations and predation treatment combinations. Proportion alive at the conclusion of the experiment used as a covariate. Dotted lines represent median developmental lifecycle stage among the treatment groups, and were again calculated over all treatment groups

## Discussion

Tradeoffs between acquiring limited food resources while avoiding predation occur regularly for most animals in natural environments (Price et al. 1980; McNamara and Houston 1987; Leibold 1989; Ludwig and Rowe 1990; Lima 1998a, 1998b), with consequences for the evolution of age and size at maturity (Abrams and Rowe 1996). In experimental studies designed to observe behavioral interactions between spiders and their grasshopper prey, the mere presence of the predator consistently modifies activity budgets of grasshoppers, increasing antipredator tendencies at the cost of reduced foraging efficiency (Rothley et al. 1997; Schmitz et al. 1997; Danner and Joern 2003). Reduced foraging efficiency as a result of increased antipredator behavior may act as a mechanism for retarded lifecycle expression, specifically growth, development, and survival (maintenance). In this study, we demonstrated that a perceived risk of spider predation

significantly decreases survival, growth, and developmental rates in nymphs of a common grasshopper species. Furthermore, we reveal the importance of high quality food availability and its potential to act in a compensatory manner, thus dramatically modifying anticipated life history responses of grasshoppers when avoiding spider predators. These results may have consequences for the evolution of age and size at maturity, as we document options that affect foraging efficiency or release consumers from competitive interactions, key assumptions in the model of Abrams and Rowe (1996).

Nonlethal effects of lycosid spiders negatively affected grasshopper performance in both years of the study in similar ways, even though general weather conditions were very different. Survivorship (Fig. 2), developmental rate (Fig. 3), and growth (Fig. 4) were significantly and negatively affected by nonlethal effects of spider predation. In a separate study designed to quantify modified behavior of *A. deorum* caused by indirect spider predation risk (Danner and Joern 2003), grasshoppers spent less than 1% of their time foraging and devoted nearly 78% of their time to defensive postures during the third instar, in comparison to grasshoppers in control treatments without spiders that only spent 44% of their time in these same defensive activities and about 5–7% of the time foraging actively. The behavioral modification caused by spider predators during stages at which grasshoppers are most susceptible probably leads to reduced food intake and increased probability of mortality (see also Beckerman et al. 1997; Rothley et al. 1997; Schmitz et al. 1997).

Increased food quality can ameliorate the negative impacts of behavioral modification caused by indirect spider predation risk. In both years, there was no difference in developmental rate and growth for grasshoppers eating ambient (relatively low) quality food in the absence of a spider versus those allowed to eat high quality food while exposed to predator risk (Figs. 3 and 4). It appears that higher quality meals compensate for lower intake rate. When coupled with direct predation, spiders may significantly alter the population dynamics of grasshoppers by directly and indirectly increasing the probability of mortality (Belovsky and Joern 1995; Belovsky and Slade 1995).

Although responses of grasshoppers to experimental treatments were similar between years, different equilibrium cage densities and treatment effects were observed (Fig. 2), in part reflecting differences in precipitation and its effect on nutrient quality of aboveground vegetation between years (Fig. 1). It is also possible that the increased duration of exposure of grasshoppers to spiders in 2002 may have contributed to differences as well. Most of the mortality we observed in 2002 occurred during the third instar, when the grasshoppers were smallest and most susceptible to predation risk. However, because we began experiments with fourth-instar nymphs in 2001, the two possibilities are confounded.

Combined, our results extend conclusions of Schmitz and colleagues for the grasshopper *Melanoplus femurrubrum* (Beckerman et al. 1997; Rothley et al. 1997;

Schmitz et al. 1997; Ovadia and Schmitz 2002), and illustrate the importance of linking food quality and predation risk to understand natural responses. *M. femurrubrum* eats both grasses and forbs, but forages in different patches determined by whether spiders are present or not. Preferred grasses are eaten when spiders are absent; when spiders are present *M. femurrubrum* moves into less preferred forb patches to feed, which also provides a refuge from predation. Forbs typically have higher protein concentrations than grasses, but also sequester defensive chemicals that act as feeding deterrents or toxins (Bernays and Chapman 1994), perhaps making forbs a less preferred host species. However, in the presence of spiders, it appears that the risk from predators while foraging outweighs the relative nutritional ranks and the grasshopper switches its diet. It appears that *M. femurrubrum* was able to eat sufficient but different food in order to maintain maintenance and growth needs in the forb habitat, since growth and development of *M. femurrubrum* was unaffected by exposure to spider predators. A strong response to spider presence was seen for *A. deorum* in this study in part because it does not have an alternative foraging habitat of nearly equal food quality that reduces predation risk. However, both studies point to the same general framework that underlies the impact of an interaction between predation risk and food quality. The different outcomes reflect different options available to the two grasshopper species rather than significantly different conclusions.

Grasshoppers and spiders play important roles in grasslands (Van Hook 1971; Mitchell and Pfadt 1974; Hewitt and Onsager 1983; Belovsky and Slade 2000), often exhibiting high diversity and dominance. Interactions with each other have the potential to both directly and indirectly affect other species within a grassland ecosystem (Van Hook 1971; Joern 1982; Cherrill and Begon 1989; Joern and Gaines 1990; Ritchie and Tilman 1992; Schmitz et al. 1997; Oedekoven and Joern 1998, 2000), including effects on grassland structure and function at several levels. Our results illustrate the complexity of recognizing possible compensatory mechanisms underlying growth and developmental responses resulting from altered foraging efficiency from nonlethal spider predation during susceptible lifecycle stages (Abrams and Rowe 1996; Oedekoven and Joern 1998, 2000; Abrams and Schmitz 1999). Furthermore, we show the importance that resource quality plays in compensating for reduced food intake caused by the interaction between wolf spiders and immature grasshopper prey. More generally, others have shown that these kinds of responses can greatly influence trophic cascades, such that indirect lethal and nonlethal impacts of spider predation on herbivores can reduce plant biomass (Schmitz 1994, 1997, 1998). As such, this study provides additional support for the notion that variation in individual responses coupled to local environmental heterogeneity can have significant effects on population, community, and even ecosystem level dynamics (Belovsky

ky and Slade 2000; Ovadia and Schmitz 2002; Schmitz 2003).

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