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PLANT QUALITY AND SPIDER PREDATION AFFECTS GRASSHOPPERS (ACRIDIDAE): FOOD-QUALITY-DEPENDENT COMPENSATORY MORTALITY

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Abstract. For insect herbivores, population responses reflect interactions among multiple factors, including abiotic conditions, food plant availability, and biotic interactions guided by food limitation and natural enemies. In this set of field experiments, we evaluated the interactive, dynamic effects of limited food supply and predation from wolf spiders (Lycosidae) on mortality in *Ageneotettix deorum*, a common grasshopper (Acrididae) from North American sandhills grasslands. We attempted to determine whether the combined effects of food availability and spider predation on mortality were (1) noncompensatory, with the effects of each factor summing to determine ultimate population size, or (2) compensatory, where the effect of one mortality factor alters the impact of subsequent factors so that the ultimate population size changes little, despite variation in specific sources of mortality. We also investigated whether changes in nutritional quality encountered by grasshoppers would result in different dynamic responses to predation in the context of noncompensatory vs. compensatory responses.

Both food availability and predation risk contributed to mortality rates. Individuals of *A. deorum* were food limited. Survival of grasshoppers feeding on fertilized plants was 50% higher than that of grasshoppers feeding on unfertilized plants over a 31-d period. Most of the mortality due to limited food occurred 12–14 d into the experiment. Predation from lycosid spiders decreased the numbers of individuals by 49% in the first 10–15 days of the experiment.

Either noncompensatory or compensatory responses resulted from the combined effects of food availability and predation on population size, depending upon the nutritional status of host plants. At ambient-level food quality (no fertilizer), spider predation and food limitation were compensatory; the same numbers of grasshoppers were recovered in treatments with and without spider-predation risk after 31 d. However, with higher food quality (N fertilizer), spider predation reduced the numbers of surviving individuals as compared with the no-spider-predation treatment, a noncompensatory response. In separate, pre-planned experiments, individuals surviving spider-predation treatments lived longer than did individuals protected from spider predation when they were caged individually over vegetation of ambient quality.

Combined, these experiments emphasize the importance of food quality as a determinant of how this predator–prey system responds, and the results suggest a mechanism underlying the response. After predation, survivors are likely to encounter more food per capita and to exhibit higher individual quality, which promotes longevity, presumably from reduced competition. This leads to a compensatory response. Under high food quality regimes, predation and food probably act in a noncompensatory fashion because grasshoppers are less food limited, and the release of additional food on a per capita basis by predation has less effect on the subsequent number of survivors.

Key words: *Ageneotettix deorum*; *developmental rates*; *food chain*; *food limitation*; *food quality*; *grasshoppers*; *herbivory*; *lycosid spiders*; *mortality*, *compensatory vs. noncompensatory*; *Nebraska sandhills grassland*; *predator–prey interaction*; *stage-specific responses*.

INTRODUCTION

Both predator-mediated processes and competition affecting insect herbivores may contribute to population and community-level interactions (Lawton and Strong 1981, Strong et al. 1984, Belovsky and Joern

1995, Cappuccino and Price 1995, Denno et al. 1995). Interactions among plants, herbivores, and natural enemies provide a variety of possible endpoints in species composition and densities, incorporating widely diverse mechanisms (Price et al. 1980, Denno and McClure 1983, Schultz 1983, Faeth 1987, Strauss 1987, Letourneau 1988, Hare 1992, Hunter et al. 1992, Hacker and Bertness 1995, Schmitz 1997, Schmitz et al. 1997, Stiling and Rossi 1997). The effects of predation

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on prey populations can be direct, resulting in lower population sizes (Hassell 1978, Carey 1993, Begon et al. 1996) or indirect, leading to an often unpredictable range of prey population responses resulting from third-party interactions (Hunter et al. 1992, Schmitz 1997, Schmitz et al. 1997). Alternately, food can regularly limit insect herbivores (Dempster and Pollard 1981, Ritchie and Tilman 1992, Belovsky and Slade 1995, Denno et al. 1995). Furthermore, considerable spatial, seasonal, and among-year variation in food availability may drive the population dynamics of insect herbivores in ways that reflect their nutritional landscape (Dempster and Pollard 1981, White 1993). Overall, food quality and availability often underlie resulting herbivore dynamics (Belovsky 1986*a, b*, Schmitz 1997, Schmitz et al. 1997, Stiling and Rossi 1997).

Underlying the range of population responses to species interactions is the specific dynamic mechanism mediating the combined effects that food limitation and predation exert on final population densities. Population-level responses to multiple biotic factors affecting mortality can be noncompensatory, compensatory, or depensatory (Anderson and Burnham 1978, Campbell and Torgersen 1983, Burnham and Anderson 1984, Connell et al. 1984, Washburn et al. 1991, Crawley 1992, Jensen 1992). An increase in one source of mortality in a natural population may or may not increase the overall mortality experienced throughout the entire life cycle. The response depends on whether the sources of mortality act in a noncompensatory or compensatory fashion (Washburn et al. 1991, Bartman et al. 1992). Noncompensatory mortality implies that additional risks of death increase total mortality in proportion to their strength, causing overall mortality to increase (Nichols et al. 1984, Kautz 1990; Fig. 1a). Any additional risk of death adds proportionally to the overall mortality rate (Washburn et al. 1991, Bartman et al. 1992). In contrast, compensatory mortality refers to a process where additional risk of death from one factor is balanced by subsequent decreased mortality from other causes in such a way that the overall mortality of the population does not change, or at least changes less than expected based strictly on noncompensatory contributions (Fig. 1b). The number of individuals surviving remains constant because of a subsequent decrease in other forms of mortality as other interactions within the population compensate for additional mortality risks (Washburn et al. 1991, Bartman et al. 1992).

Host-plant quality may ultimately alter the impact of natural enemies on herbivore prey at both individual and population interaction levels through effects on fecundity, survivorship, growth rate, and development rate, thus changing the abundance, renewal rate, and age or size structure of the herbivore population. For example, reductions in herbivore development rate may increase (Loader and Damman 1991) or decrease (Clancy and Price 1987) vulnerability to natural enemies.

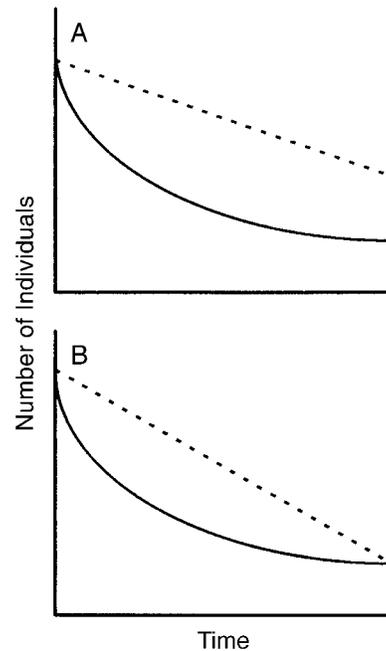


FIG. 1. Hypothetical trajectories of surviving individuals over time in a population showing (A) noncompensatory and (B) compensatory responses. Treatments are no predation (---) and predation (—).

Increased population growth rate due to changes in fecundity or survivorship can reduce the impact of natural enemies (Werner 1991, Hanks and Denno 1993). Impaired growth or lower developmental rate from eating poor-quality food do not necessarily lead to direct changes in herbivore mortality (Damman 1987), but prolonged exposure to predators or reduced escape efficiency can increase mortality resulting directly from predation rather than starvation (Price et al. 1980, Schultz 1983). In natural settings, variable host-plant quality is the norm, lending additional importance to its influence on insect herbivore populations.

Variable host-plant quality may also influence predator-prey interactions by changing the spatial and temporal distribution of the prey (Hassell and Southwood 1978, McClure 1983, Schultz 1983, Heidorn and Joern 1987, Stiling and Rossi 1997). Aggregation in high-quality patches may either increase or decrease the predation risk, depending on the predators' numerical and functional responses to altered growth rate or prey distribution (Hassell 1978, Chesson and Murdoch 1986, Damman 1987, Walde 1995).

Individuals seldom exploit resources identically (Begon 1984, Lomnicki 1988), and certain individuals typically obtain more of the available resources than others. The number of individuals that reproduce and ultimately contribute offspring to the next generation will depend both on how many resources are available and how they are apportioned among individuals in the population, an issue of individual quality (Begon 1984,

Wall and Begon 1987, Lømnicki 1988). Differences in individual quality and the ability to garner resources may either be genetically based or merely reflect chance access to resources at a critical point in the life cycle. The critical point is that differences in individual quality translate into corresponding differential survival (Lømnicki 1988).

Using field experiments, we examined the potentially interactive roles of food-plant quality and spider predation on growth and survival by *Ageneotettix deorum* Thomas, a grass-feeding grasshopper common to many western North American grasslands. Historically, the dynamics of grasshopper populations, especially nymphal mortality, have largely been attributed to variations in climate (Dempster 1963, Uvarov 1977). The central importance of biotic interactions in grasshopper dynamics has only recently been emphasized (Joern and Gaines 1990, Belovsky and Slade 1993, 1995, Belovsky and Joern 1995), although Greathead (1963) recognized the possibility. Single-factor field experiments document competition from food limitation (Schmitz 1993, 1994, Belovsky and Slade 1993, 1995, Joern and Klucas 1993, Denno et al. 1995, Evans 1995). Other experiments show that natural enemies may strongly affect grasshopper populations (Kajak et al. 1968, Chapman et al. 1979, Joern and Rudd 1982, Joern 1986, 1988, 1992, Belovsky et al. 1990, Fowler et al. 1991, Bock et al. 1992, Belovsky and Slade 1993, 1995). It is increasingly clear that both food limitation and predation interact to influence grasshopper population processes (Belovsky and Joern 1995). We must now focus on the way in which these two factors influence one another. Better understanding of the interaction between food competition and predation will provide important insights about mechanisms underlying ecological patterns.

We examined two related hypotheses with field experiments. (1) Food limitation and spider predation will have compensatory effects on *A. deorum* numbers. If this is true, then as a possible mechanism, we hypothesize that (2) reduced population size from spider predation will increase future per capita survival because the individual quality of survivors will increase over that of individuals in the absence of predation, even over short exposure periods. This increase in individual quality presumably results because of the increased availability of highly nutritious food to survivors in predation treatments.

MATERIALS AND METHODS

Study site

We conducted field experiments in 1994 and 1995 at and near Arapaho Prairie, a research preserve in the southwest portion of the Nebraska sandhills grassland (Arthur County). Arapaho Prairie represents typical upland dry sandhills prairie, with steep slopes grading into undulating dunes and flat valleys. Approximately

200 plant species occur at this site, of which about 80% of the taxa are forbs, but 80% of the biomass and structure is provided by grasses (Keeler et al. 1980, Barnes et al. 1982).

Similar grasshopper assemblages routinely exist throughout the site and in neighboring grazed areas (Joern 1982). Densities of grasshoppers vary in both time and space, but combined species densities average about 3–4 adults/m². During years when outbreaks occur (every 7–10 years), combined adult densities can be 6–7 times higher in some patches; 15–40 nymphs/m² are regularly observed in specific patches, even in years with average adult densities (Joern and Pruess 1986; A. Joern, *unpublished data*). Experiments were designed with these densities in mind.

The grass-feeding grasshopper *Ageneotettix deorum* commonly occurs throughout western and central U.S. grasslands, particularly in association with grama grass species (*Bouteloua*) (Pfadt 1994). At Arapaho Prairie, this species typically hatches in early to mid-June and becomes adult by mid-July. *Bouteloua* grasses predominate in its diet (Joern 1985), although other grasses are also eaten. Significant within- and among-year variability in nutritional quality of dominant grasses exists at Arapaho Prairie (Fig. 2a). It is not uncommon for total foliar N to range from 5 to 6% early in the growing season and drop to below 1% total N by late July or early August in some years, with significant among-year and species-specific differences in percentage total N (Fig. 2b).

Grasshoppers at Arapaho Prairie and in other grasslands are readily eaten by both vertebrate (primarily birds) and arthropod predators (including robber flies and especially spiders) (Joern and Rudd 1982, Joern 1986, 1988, 1992, Belovsky and Slade 1993, 1995, Oedekoven and Joern 1998). Spiders are common and diverse at Arapaho Prairie (Oedekoven 1996), but their quantitative impact on grasshoppers or other insect prey is generally unknown at this site. The most common wandering lycosids at the site are in the genus *Schizocosa*. A related study demonstrated pronounced, stage-specific risk of mortality for the dominant grasshopper species from this wandering spider guild on grasshoppers at this site (Oedekoven and Joern 1998). These field experiments showed that nymphs were most vulnerable to spider predation (whereas adults were almost completely unaffected), and that mortality levels of younger, smaller nymphs from all causes were considerably greater than those of older, larger nymphs (93% mortality for third-instar nymphs vs. 64% mortality for fifth-instar nymphs) (Oedekoven and Joern 1998). Overall, spider predation contributed about 17–23% to the total mortality at each nymphal stage considered separately in field experiments under ambient environmental conditions.

Basic experimental plan

We caged *A. deorum* nymphs over naturally occurring vegetation, and then tracked survivors in field ex-

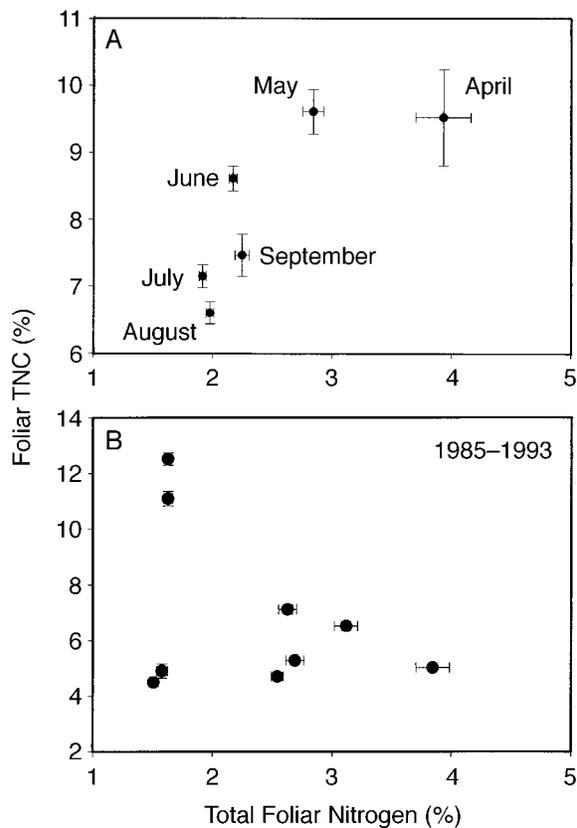


FIG. 2. Variability in grass nutritional quality at Arapaho Prairie, Nebraska, 1985–1995. (A) Average monthly values (± 1 SE) (April–September) of percentage total nitrogen and total nonstructural carbohydrates (TNC) of leaf tissue samples for seven common graminoid species at Arapaho Prairie (*Agropyron smithii*, *Andropogon hallii*, *Andropogon scoparius*, *Bouteloua gracilis*, *Calamovilfa longifolia*, *Carex heliophila*, and *Stipa comata*). (B) Average annual leaf concentrations (± 1 SE) of percentage total nitrogen and TNC for the seven grass species listed above.

periments to determine the relative contributions of variable host-plant quality and predation from lycosid spiders to final grasshopper mortality. We used a randomized, complete-block 2×2 factorial design experiment that manipulated (a) food quality (presence or absence of N-P-K fertilizer), and (b) lycosid spider predation, using semipermeable cages (spider predation vs. no spider predation).

Food quality was elevated beyond ambient levels in half of the cages with Miracle Gro N-P-K (15-30-15) fertilizer at 10 g N/m², added at half-strength in 1 L water per cage on two occasions about 1 wk apart at the beginning of the growing season in June. Nonfertilized plots received water only. Fertilizer levels were chosen based on past studies at this site that manipulated N levels within this range, significantly raising the protein levels of the primary species of grasses eaten by *A. deorum* (Heidorn and Joern 1987, Joern and Alward 1988). Like many grasshoppers, *A. deorum*

responds positively to increased plant protein levels (Behmer and Joern 1993, 1994, Yang and Joern 1994, Joern and Behmer 1997, 1998), resulting in lowered food-processing rate and increased survival and egg production rate.

Cages were constructed of wooden frames (0.25 m² basal area \times 0.75 m high) that either prevented or permitted the entry of wandering lycosid spiders. Cage design restricted access by spiders in no-predation treatments. Spiders were excluded from cages constructed entirely of fine (1-mm) mesh screen through which spiders could not pass. Semipermeable cages that permitted entry by spiders were constructed of fine-mesh screen except for a 20 cm high band of 3-mm mesh placed at ground level around the entire cage perimeter. Our cage size represents a compromise, based on experience, between using the largest possible cage to permit free movement by individuals and using a cage small enough to allow us to accurately census individuals trapped inside. Other experiments demonstrated ready access of spiders into these cages while confining grasshoppers, 95% of which had body lengths <15 mm (Oedekoven and Joern 1998). In laboratory experiments, all third-instar and older grasshoppers could not pass through the mesh cages, while first- and second-instar individuals readily escaped. All lycosid spiders <15 mm in length readily moved in and out of 3-mm mesh cages, and all spiders >8 mm in length readily attacked and consumed nymphs of all stages in laboratory trials (Oedekoven and Joern 1998). At the onset of the experiments, we placed cages over arbitrary patches of similar vegetation within each block, secured them, and randomly assigned treatments to cages. This experiment adequately incorporates inherent variability within the study system; blocks were located throughout a larger 1180-ha region representing multiple dunes and valleys, with no block closer than ~400 m.

Experiment 1: Noncompensatory vs. compensatory response

In 1994, we initially stocked cages with eight fourth-instar nymphs and tracked survivorship by censusing approximately every other day for 31 d (18 measurements/cage over this period). Stocking densities represent realistic levels on the somewhat high end of naturally observed densities based on 20 yr of data (Joern and Pruess 1986; A. Joern, unpublished data). At the end of the experiment, grasshoppers were adults for approximately 10 d. Each treatment was replicated at each of 12 blocks arbitrarily located over a range of vegetation types encountered at this study site.

To distinguish between noncompensatory and compensatory responses, we compared the final number of individuals for each treatment (Fig. 1). If no differences in numbers of surviving individuals existed between the two fertilizer treatments across predation treatments, then we judged the response as fully compen-

satory. Significant differences in final grasshopper numbers indicate noncompensatory (or partially compensatory) responses. While it is possible for the responses to lie somewhere between fully noncompensatory and fully compensatory, we could not quantitatively assess partial compensation. The actual survival trajectories for different treatment combinations most likely differ (Fig. 1), indicating that there may be many possible ways to end up with the same population densities. Trajectories are most informative in providing mechanistic understanding of either noncompensatory or compensatory responses.

We employed a factorial, randomized, complete-block ANOVA (12 replicates/treatment) (Cochran and Cox 1957, Mead 1988). Main effects included spider predation (cage type) and N fertilizer, with repeated measures of the number of grasshoppers for each cage over the 31-d period for these 48 units. We examined the number of survivors in cages at the end of the experiment to distinguish between noncompensatory and compensatory mortality (Fig. 1). We performed statistical analyses with natural log-transformed values of number of individuals to highlight changes in mortality rates of caged populations. We used repeated-measures ANOVA profile analysis (SAS Institute 1989) to evaluate differences in numbers of survivors over time in order to examine whether differences existed in the dynamics of the response by treatment. To determine at which point (if any) the mortality curves diverged, we compared differences between adjacent treatments for transformed variables with ANOVA, using Proc GLM of SAS/STAT (1989; SUMMARY option).

Experiment 2: Individual differences

A second experiment judged differences in individual quality in response to treatments using survivors of experiment 1. We expected that on a per capita basis, survivors of the spider-predation treatment would encounter more nutritious food than those in the no-predation treatment, because early-occurring mortality from spider predation released quality food to survivors. When placed in a common nutritionally limiting environment, individuals previously experiencing higher quality food should live longer than individuals formerly experiencing poorer quality food. After 31 d, survivors from each of the four treatment combinations employed in experiment 1 were placed individually in 3-mm mesh hardware cloth cages (14 cm in diameter \times 20 m tall) located over plots of *Bouteloua gracilis* under otherwise ambient conditions at a common site. We estimated individual survivorship with daily censuses.

We expected that individual quality of survivors from any treatment would be negatively related to the number of survivors in each cage from experiment 1, in addition to any effects resulting from differences caused by spider predation. Since individuals used in

this experiment came from cages with different final numbers of survivors, we analyzed results using ANCOVA, with the final number in each cage at the end of experiment 1 treated as the covariate. The covariate is not statistically significant if the response is density independent.

Experiment 3: Stage-dependent individual differences

We performed a third, two-tiered experiment in 1995 to determine whether the spider-predation treatment influenced the subsequent individual success (quality) of survivors at each of three developmental stages. Experiment 3 was very similar to the combined protocols of experiments 1 and 2, and the same cage designs were used. Differences between the protocols were as follows. Separate experiments were run in the field for fourth- and fifth-instar nymphs and adults during the seasonal period when these stages occurred naturally. In the first part of this experiment, spider predation was manipulated as in experiment 1, but for a much shorter period (10 d, the approximate length of a developmental stage) using seven replicate blocks. Subsequent survival (number of days alive) was then quantified for each survivor when caged individually over naturally occurring vegetation, as in experiment 2. Individual survival was only examined with ambient food quality; no N-fertilizer treatment was applied in this experiment. We quantified survivorship with daily censuses. We used ANCOVA to analyze the results as in experiment 2, with the final number of survivors per cage at the end of the spider-predation portion of the experiment treated as the covariate.

RESULTS

Experiment 1

Both fertilizer addition and spider predation significantly affected the number of grasshoppers remaining in cages after a 31-d period (Fig. 3, Table 1). However, the interaction between the two factors provides the most insight into key dynamic processes leading to noncompensatory or compensatory mortality. The number of grasshoppers surviving until the end of the experiment was 52% higher in the fertilizer treatments, averaged across both spider-predation treatments (Fig. 3, Table 1). Fertilizer initially had no effect on the number of grasshoppers remaining, and the two trajectories did not diverge until days 14–16 (profile analysis, $P < 0.03$, Fig. 3). After this episode of mortality, no significant differences in the slopes (mortality rates) existed between fertilizer treatments. The overall trajectories of the two fertilizer treatments after the trajectories leveled off did not differ statistically (repeated-measures ANOVA, time \times fertilizer interaction, Wilks' $\lambda = 0.38$, $F = 1.08$, $df = 11, 17$, $P = 0.46$).

Spider predation significantly decreased the number of surviving *A. deorum* by 49%, averaged across both fertilizer treatments after 31 d (Fig. 3, Table 1). An

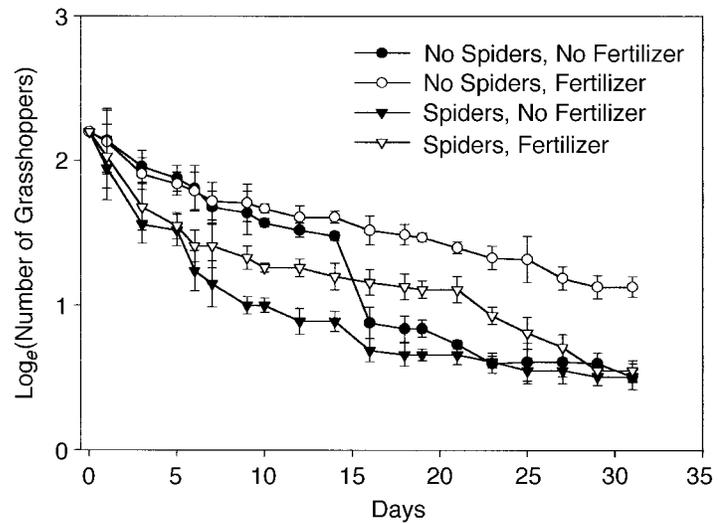


FIG. 3. Trajectory of the natural log of surviving grasshoppers (mean \pm 1 SE) for fertilizer and predation-risk treatment combinations for the duration of experiment 1.

immediate, accelerating impact on mortality from spider predation independent of fertilizer treatment was observed (repeated-measures ANOVA, time \times spider interaction, Wilks' $\lambda = 0.06$, $F = 6.36$, $df = 11, 17$, $P < 0.002$). After the initial, immediate decrease in *A. deorum* numbers, the per capita predation rate associated with subsequent spider predation was not significant.

To understand the underlying dynamics that explain mortality, both predation and food quality must be considered simultaneously (Fig. 3, Table 1). The number of survivors in the fertilized, no-predation treatment was significantly greater than in the other three treatment combinations (Fig. 3); survivors at the end of the experiment for the other three treatment combinations did not differ significantly from each other. Moreover, the trajectories of the responses ($\ln N$ over time) for each treatment combination differ in predictable ways that provide insights into the nature of compensatory vs. noncompensatory responses in mortality.

We gain additional insights when simultaneously considering the trajectories of spider predation with food limitation treatments using a repeated-measures ANOVA. There was a significant effect of food quality on the response trajectories (repeated-measures ANOVA, time \times spider \times fertilizer interaction, Wilks' $\lambda = 0.12$, $F = 4.58$, $df = 11, 17$, $P = 0.007$). In spider-predation treatments, the trajectories diverged, result-

ing in higher survivorship in cages with fertilizer compared with no fertilizer for much of the experimental period. For example, spiders reduced grasshopper numbers to a minimum threshold of approximately one individual per cage by day 16 in unfertilized cages, compared to the same density in 25 d in fertilized cages. In the fertilized cages (with spider predation), a similar drop in survival rate began at about day 21, suggesting that food limitation increased at this point. By the end of the experiment, the two treatments exhibited the same number of survivors.

Experiment 2

Individuals are often differentially susceptible to mortality from natural sources, an attribute often referred to as individual quality (Begon 1984, Lømnicki 1988). When caged singly, individual grasshoppers experiencing and surviving prior exposure to spider predation survived significantly longer in this experiment than did individuals taken from cages without risk to spider predation (Table 2, Fig. 4). More individuals survived in the fertilized plots within each predation treatment, and grasshoppers from fertilized plots subsequently lived longer in individual cages regardless of predation treatments (Fig. 4). Final grasshopper density in cages at the end of the 31-d exposure period

TABLE 2. ANCOVA for continued individual survival (number of days) after 31 days' exposure to treatments from a factorially arranged fertilizer and spider-risk experiment.

Source	df	F	P
Spider	1, 24	6.33	0.019
Fertilizer	1, 24	4.29	0.048
Spider \times Fertilizer	1, 24	0.88	0.356
Survivors/cage \ddagger	1, 24	6.44	0.018

\ddagger Number of grasshoppers alive in cages at the end of the 31-d experiment before subsequent individual assessment (survivors/cage is the covariate).

TABLE 1. Repeated-measures ANOVA for the natural log of the number of surviving grasshoppers in response to fertilizer and spider predation treatments in experiment 1.

Source	df	F	P
Block	10, 27	1.38	0.24
Spider	1, 27	11.16	0.003
Fertilizer	1, 27	8.61	0.007
Spider \times Fertilizer	1, 27	6.11	0.02

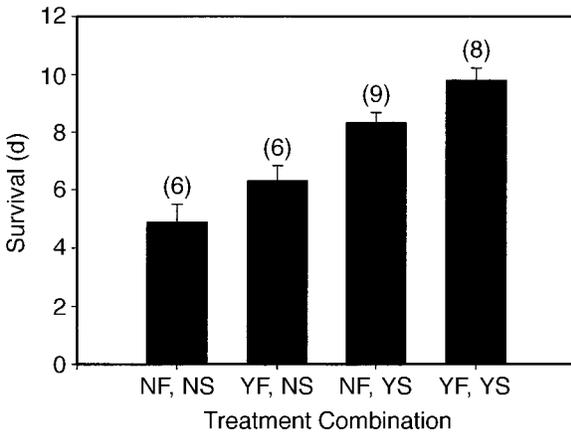


FIG. 4. Average number of days alive (+1 SE) for each combined fertilizer and spider treatment over the 31 days of the experiment. The first abbreviation of the treatment combination denotes fertilizer treatment (NF = no fertilizer; YF = fertilizer), and the second denotes the possibility of spider presence based on cage design (NS = no spider, YS = spider entry permitted). Numbers in parentheses above bars represent the sample size of the treatments.

prior to testing individual quality was used as the covariate in this analysis. The covariate significantly affected future likelihood of survival in individual trials ($P < 0.02$, Table 2) in that individual survival was lower when more grasshoppers remained alive.

Experiment 3

Overall, subsequent individual survival for *A. deorum* increased for individuals from cages exposed to spider predation for all three developmental stages tested (Fig. 5, Table 3). Grasshoppers experiencing and surviving prior exposure to spider predation lived significantly longer when caged alone than did individuals taken from cages without risk to spider predation, independent of developmental stage and length of exposure (Fig. 5, Table 3). Also, overall mortality possibly decreased in older developmental stages (Fig. 5, Table 3, $P = 0.06$).

DISCUSSION

We documented both noncompensatory and compensatory mortality in this grasshopper–spider predation system, responses ultimately dependent on plant nutritional quality (Figs. 3–4). Clearly, food limitation was important in this experiment. When ambient food levels (no fertilizer) were compared with and without spider predation, the difference in final number of grasshopper survivors was not statistically significant, showing a compensatory response. However, even though the population size at the end of the experiment was the same, the different response trajectories indicate that the underlying dynamics attributable to food limitation differed between the two predation treatments. Contrast this response with the noncompensa-

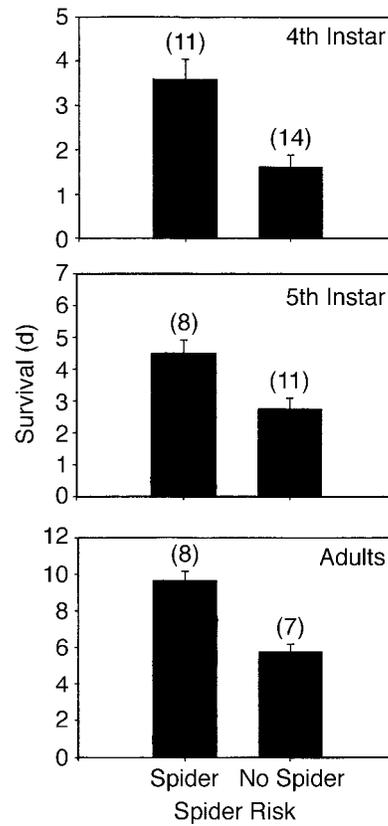


FIG. 5. Average survival of individually caged *A. deorum* for three developmental stages after a 10-d exposure to presence or absence of potential spider predation (mean number of days alive + 1 SE). Individuals were caged over natural vegetation that included *Bouteloua gracilis*. Ordinates for the three developmental stages (fourth instar, fifth instar, and adult) are scaled differently. Numbers in parentheses above bars represent the sample size of the treatment.

tory effects of mortality from spider predation observed when food quality is high in fertilizer treatments. Results illustrate subtle but important shifts in dynamic interactions between predators and prey that resulted from variation in plant nutritional quality.

Resources and predators interact to determine population- and community-level responses by herbivores (Sih et al. 1985, Paine 1988, Hunter et al. 1992, Wise

TABLE 3. ANCOVA for continued individual survival (number of days) after 10 days' exposure to spider risk treatments for three developmental stages (fourth instar, fifth instar, and adult).

Source	df	F	P
Stage	1, 22	3.9	0.06
Spider	1, 22	4.8	0.04
Spider × Stage	1, 22	2.9	0.10
Survivors/cage†	1, 22	4.4	0.05

† Number of grasshoppers alive in cages at the end of the 10-d exposure to predation risk before subsequent individual assessment (survivors/cage is the covariate).

1994, Polis and Winemiller 1996). Early hypotheses about limitation and regulation of herbivores in food webs emphasized top-down control (Hairston et al. 1960, Price et al. 1980, Oksanen et al. 1981, Carpenter 1985, Fretwell 1987). A full range of complementary top-down and bottom-up views regarding the dynamics of food web regulation now exists (Hunter et al. 1992, Power 1992, Schmitz 1994, 1997, Wise 1994, Polis and Winemiller 1996). Food web studies that focus on the responses of herbivores to manipulations at either higher or lower trophic levels routinely document dramatic responses at the herbivore level. Results support either top-down or bottom-up regulation, or more commonly, some combination of the two. Current efforts in this area focus on the relative contributions of both top-down and bottom-up processes to the final herbivore response (Leibold 1992, Power 1992, Ritchie and Tilman 1992, Schmitz 1993, 1994, 1997, Polis and Winemiller 1996, Stiling and Rossi 1997). A key unresolved problem in such studies concerns the specific nature in which multiple factors interact to determine the final density or biomass at the herbivore level. There seems to be a tendency to assume noncompensatory effects, even when a convoluted string of indirect interactions are in effect. Identifying the specific population-level mechanisms underlying these responses will greatly expand our understanding of this problem.

Grasshoppers as target organisms in these experiments are no different than other systems. In conjunction with the potentially ubiquitous influence of weather-related factors, both food limitation (Belovsky and Slade 1993, 1995, Schmitz 1993, 1994, Evans 1995) and predator-mediated processes (Kajak et al. 1968, Lawton and Strong 1981, Strong et al. 1984, Joern 1986, 1988 1992, Joern and Gaines 1990, Belovsky et al. 1990, Fowler et al. 1991, Bock et al. 1992, Belovsky and Slade 1993, Belovsky 1995, Chase 1996a, b) contribute to the dynamics and limitation of grasshopper populations. In this study, we examined specific mechanisms that underlie the interaction of both food limitation and predation risk as they interact to determine grasshopper mortality.

Our results contribute directly to current efforts to disentangle the relative influences of bottom-up vs. top-down factors in terrestrial food chains (Schmitz 1993, 1994, 1997, Wise 1994, Moran et al. 1996, Schmitz et al. 1997). We found that both food limitation and spider predation interact in contributing to mortality in *A. deorum*. However, the nature of the contributions of each factor to final density differed, and the actual mechanism (noncompensatory or compensatory responses) depended on food quality. Since availability of quality food influenced both the final response and the type of interaction between food and spider treatments, we conclude that food limitation, a bottom-up factor, contributed importantly to the mortality observed in the present study, even when spider predation proved significant. In a broader context, food quality set the stage

for the response to predation (i.e., it acted as an important environmental state variable), a result consistent with that reported by Stiling and Rossi (1997).

Noncompensatory and compensatory responses

When multiple factors contribute to population abundances, it is critical to understand the underlying interactions among factors (Belovsky and Joern 1995). While multiple sources of mortality affect natural grasshopper populations, it is not yet clear how each contributes to limitation and regulation of natural populations, or how these factors affect the action of one another (Joern and Gaines 1990). The compensatory mortality hypothesis predicts that early-occurring mortality from spider predation will replace subsequent per capita mortality of grasshoppers from other sources, as long as spider predation intensity falls below some critical upper threshold. Under this scenario, the final population density will remain unchanged after one source of mortality has been eliminated, because other sources of mortality increase proportionally in their impact. The noncompensatory mortality hypothesis, on the other hand, predicts that spider predation coupled to mortality from food limitation will result in reduced densities because both spider predation and other sources of mortality act in a largely independent and therefore noncompensatory fashion (Ellison 1991).

Final population densities in our experiments were either noncompensatory or compensatory, depending on environmentally determined food quality. When quality food was readily available to *A. deorum* in the fertilizer addition treatment, mortality accruing from resource limitation and spider predation was noncompensatory. With no spider predation, the number of survivors at the end of the experiment in fertilized cages was somewhat more than twice that of unfertilized cages. A key to understanding the response is the significant drop in survivorship in the nonfertilized, no-predation treatment during days 14–16 compared to the fertilized, no-predation treatment. Prior to this point, the survivorship curves between the two food quality treatments (with no spider predation) are indistinguishable in number of survivors and in slope of the response. After the die-off in the nonfertilized treatment, the slopes of survivorship for the two treatments again are similar. These responses support the hypothesis that grasshoppers in nonfertilized cages literally ran out of quality food to support such a high population at day 14, and populations dropped by about half over a 2–3-d period before leveling off again. These results also suggest that grasshopper populations caged with fertilized plants do not deplete food resources below a critical threshold level that causes high levels of starvation. Predation pressure, coupled with other sources of mortality, reduces the population density in a noncompensatory fashion.

When the availability of quality food lies below some critical threshold that by itself results in high levels of

starvation, the combined effects of food and predation interacted in a compensatory fashion as final densities did not differ between the two spider-predation treatments when plants were not fertilized. Two observations explain this result. First, food determines the number of individuals that can persist in this environment and excess individuals will starve. Second, the relative timing of mortality from the two factors is important. Spider predation occurring early in this sequence reduces population levels below this critical starvation level, which increases food availability on a per capita basis. For compensatory mortality to occur, predation must precede starvation; late predation occurring after significant death has already occurred from food limitation will result in a noncompensatory response. This result is noteworthy because this observed response corresponds to naturally occurring host-plant availability and quality, and ambient levels of spider predation. For this reason, we expect mortality levels associated with spider predation and food quality to often be compensatory under natural conditions, a result observed for different grasshopper species in Montana Palouse grassland (Belovsky and Slade 1993).

Consequences of spider predation for individual grasshopper performance

Spider predation can contribute significantly to grasshopper mortality through direct and indirect impacts on nymphal stages (Table 1, Fig. 3; Kajak et al. 1968, Schmitz 1993, 1994, 1997, Schmitz et al. 1997). One clear effect of predation is that it reduces the number of individuals in a population. One issue important for understanding the true role of predation concerns the related consequences of reducing population size. For example, reducing competition decreases demand on limited resources from that point on, thus allowing remaining individuals access to more food of higher quality, enabling them to survive longer. Results of experiments 2 and 3 suggest that such interactions exist between spider predation and *A. deorum*'s nutritional state. Ultimately, an individual's capacity to acquire and store nutritional resources defines individual quality and will affect subsequent survival. Our results are consistent with our second hypothesis, although we need more detailed information before we can completely resolve the specific underlying physiological and behavioral mechanisms. This hypothesis inspired experiments 2 and 3 prior to their execution.

When food resources were most limiting in these experiments, increased density dependence from competition limited the ability of individual grasshoppers to locate and consume enough food of sufficient quality. Any factor, such as predation, that reduces the overall number of grasshoppers selecting food from the same limiting resource pool will result in more food for each survivor. Because of the effects of predation, fewer grasshoppers consuming high-quality food

means that each surviving grasshopper will obtain a higher quality diet, with consequent positive impact on demographic performance (e.g., survival, developmental rate, growth rate, and fecundity), as described by Lomnicki (1988). Demographic performance by *A. deorum* responds directly to increased protein content in their food (Joern and Behmer 1997), the kind of response expected in these experiments, because sufficiently high levels of protein on a per capita basis would be available for an extended period. Schmitz et al. (1997) document a similar risk of starvation among individual nymphal grasshoppers, which illustrates how sensitive grasshoppers are to food shortage for related reasons. Further testing about whether the specific mechanism proposed here explains the combined results of these three experiments will require more explicit estimates of per capita food availability and quality, coupled to understanding of how food reserves are stored and used by grasshopper nymphs to affect future survival. These data are not currently available.

Important insights about the roles of direct and indirect effects of biotic interactions on community dynamics result from numerous manipulations of many systems. Our experiments clarify the fact that processes occurring at both individual and population levels are involved in determining final population numbers, adding to comprehensive statements regarding interactive population processes in grasshoppers (Belovsky and Joern 1995). Moreover, the nutritional state of host plants encountered by *A. deorum* nymphs greatly influences mortality rates and final population sizes in more than one way. Interpretations of species deletion or augmentation experiments as they affect population and community processes are often not clear-cut, especially in complex situations (Schmitz 1997), and the specific nature of such underlying mechanisms becomes important, as identified in this study. Our results provide mechanistic insights that will help make future interpretations and predictions more accessible and even predictable, and we hope they will lead to better understanding of community organization.

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