Stage-based mortality of grassland grasshoppers (Acrididae) from wandering spider (Lycosidae) predation

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Abstract — Mortality rates in insects, including grasshoppers (Acrididae), are often stage- or size-specific. We estimated stage-specific mortality rates for three common grasshopper species from a Nebraska (USA) sandhills grassland (Ageneotettix deorum, Melanoplus sanguinipes and Phoebolites nebrascensis), and partitioned the impact due to wandering spider predation from remaining sources. Survivorship was estimated for multiple developmental stages (3rd instar through adult) under experimental conditions that either prevented or permitted predation from free-living, wandering spiders (primarily Schizocosa species). Total stage-specific mortality, including spider predation, examined over the period of single stages was greatest for the youngest stages (91 % for 3rd instar, 73 % for 4th instar, 63.5 % for 5th instar and 30.4 % for adults). For the developmental stages considered and averaged for all species, the contribution to total mortality from spider predation over the 10-d period (approximately the length of a developmental stage) ranged from 17 % for 3rd instar nymphs to 23 % for 4th and 5th instars, and an undetectable level for adults. While spiders may depress grasshopper numbers, contributions from spider predation to grasshopper population dynamics are uncertain. © Elsevier, Paris

Ageneotettix deorum / field experiment / grasshopper population dynamics / Melanoplus sanguinipes / Nebraska sandhills grassland / Phoebolites nebrascensis / Schizocosa spp. / stage-based survivorship

1. INTRODUCTION

Mortality and its causes are not equally distributed among developing stages throughout the life cycle of most insects. In particular, the youngest individuals typically experience the greatest mortality (stage-dependent mortality) [8]. Equally significant, specific causes of mortality operate differentially among stages. In grasshoppers, for example, death from starvation may be more likely in young nymphs, while adults may be at greater risk from other factors such as avian predation [4]. Partitioning the actual causes of total mortality among developmental stages provides critical information for understanding both the evolution of life histories as well as the dynamics underlying population change [8, 15, 46].

Predator-mediated interactions can play important roles in shaping prey-species characteristics, including growth rate, body size, physiological constraints, mating behavior, ontogenetic patterns of resource allocation, habitat use, movement patterns, escape behavior, abundance, and morphology [10, 46, 48, 54, 60]. Predation often contributes to both population fluctuations as well as community level patterns and processes [31, 36, 51, 52, 57]. In particular, different age- or stage-classes may experience different susceptibilities to predation, often in a size-selective manner. Since most insects develop through a series of size-varying stages, size-dependent processes such as predation can play important roles in their life history and population processes [15, 42].

In this field experiment, we assessed patterns of stage-specific risk to predation on three common grasshopper species from wandering spiders (Lycosidae) relative to other sources of mortality. While much of the theory for arthropod predator-prey relations involves specialist predators and parasites, or interactions among only a few species, many arthropod predators exploit a variety of prey [21, 45, 61]. Within guilds of generalist predators, omnivory, interspecific predation, exploitative or interference competition, and cannibalism may occur [18, 43, 44, 56]. The complexity arising from such interactions among generalist predators compared with specialized
predators leads to qualitatively different responses in theoretical models [21, 22, 45]. Similarly, numerous field experiments demonstrate that indirect interactions among generalist predators have complex effects on prey assemblage dynamics [16, 24, 25, 35, 31–53, 55, 62].

Field observations and experiments often support the hypothesis that spiders can limit insect densities [37, 47, 49, 59, 61], but not always [26]. However, the degree to which spiders limit insects in most ecosystems is largely unknown [61]. Spiders are typically generalist predators, eating most arthropod prey encountered if they are capable of doing so [38, 47, 49, 61]. Because most spiders are not prey specialists and have long generation times relative to most of their insect prey, individual spider species may not exhibit population-level, density-dependent tracking of their prey, but rather switch to the most common suitable prey [49]. Energy-flow studies indicate that spiders can take a large fraction of the available insect herbivores, often between 20–44% of the total net herbivore/omnivore insect production [37, 59]. These figures possibly underestimate the potential effect of spiders on population processes because not all prey encountered in these studies were suitable; due to either size or palatability [61]. Stronger support, that spiders limit prey numbers, comes from experimental studies that document the potential for overall insect prey limitation by spiders over short periods [33, 45, 47, 49, 61], but it is not always observed [3, 4, 26].

Grasshoppers (Orthoptera: Acrididae) are frequently the dominant, large insect herbivores in North American grasslands [23]. While the dynamics of grasshopper populations have been traditionally attributed to the vagaries of climate [4, 14, 58], field experiments have repeatedly shown that biotic interactions [2–4, 31] including vertebrate and invertebrate predation may affect grasshoppers populations [3, 5, 6, 9, 17, 19, 28–30, 32, 33]. With some exceptions [3, 51–53], differential stage-based mortality from predation has not been specified for this group, despite the clear importance of stage-specific mortality for understanding grasshopper population dynamics [2, 8, 31].

Using field experiments, we examined the following questions concerning stage-selective risk to predation on grasshopper nymphs. First, what is the nature of stage-dependent mortality by grasshoppers from natural grasslands and what proportion can be attributed to predation from wandering spiders? Second, at what stage, if any, do grasshoppers escape predation, and if so, what are the implications? Third, are common grasshopper species equally susceptible to stage-specific predation from wandering spiders? Results from our experiments reinforce the need to address different sources of mortality in a stage-dependent fashion in population models.

2. MATERIALS AND METHODS

2.1. Study site

All field experiments were conducted at and near Arapaho Prairie (Sections 31, 32; T18N, R39W) in the southwest portion of the Nebraska sandhills in Arthur County (USA). Arapaho Prairie is typical upland sandhills prairie where dry sandhills have steep slopes grading into undulating dunes and then flat valleys. Approximately 200 plant species occur at this site, of which about 80% are forbs. Grasses constitute about 80% of the above-ground biomass and provide most of the structure [1, 34]. Arapaho Prairie is maintained as an experimental research reserve and is not typically grazed although periodic mowing at 4-year intervals occurs in valley regions. All neighboring land parcels are regularly grazed by cattle but vegetation is similar in structure and species composition, except for the expected grazing-induced effects.

Grasshopper assemblages vary somewhat in relation to the vegetation type but most species are found throughout the area [27]. Densities of grasshoppers are variable in both time and space, but adult densities average around 3–4 individuals m⁻² except during years when outbreaks occur (every 7–10 years) at which time, densities can be much higher [27]. Total nymphal densities from 15–40 individuals m⁻² are regularly observed in specific patches in many years, and adult densities can reach these densities in local patches. Only a small fraction of the available grasshopper species predominate in most years; 3–5 species (out of about 30 species present) typically constitute 80% of the individuals present (Joern, unpubl. data).

During the summer of 1994, we measured stage-specific mortality rates of three common grasshopper species, Aeneotettix deorum Scudder, Melanoplus sanguinipes (Fabr.), and Phoebatopsis nebrascensis Thomas in a natural setting. All three species are common at Arapaho Prairie as well as in Nebraska sandhills grassland generally. Grasshopper species typically emerge at different times throughout the season, and species used in this study emerge in the above order [7], with phenologies successively displaced by as much as 2–4 weeks apart. However, much variation in the actual timing of emergence and development exists among years at this site (Joern, unpubl. data). In 1994, the phenological appearance of these species appeared in such a way that the same stages in all three species overlapped under natural conditions. This allowed us to assess among-species differences in risk for spider predation without further confounding it with seasonal effects.

Although the entire wandering spider guild may contribute to any observed responses in these experiments, the most common spider species (Lycosidae).
Grasshopper Developmental Stage

Figure 1. Grasshopper body length (mm) by developmental stage for individuals from naturally occurring populations in 1994. Bars represent means (± 2 standard errors). Regressions for body length on developmental stage (X) for each species are: *Agenetaetis deorum* (Y = 0.257 + 0.229X, \( R^2 = 0.834 \)), *Melanoplus sanguinipes* (Y = 0.331 + 0.3009X, \( R^2 = 0.85 \)), and *Phaeticotes nebrascensis* (Y = 0.3439 + 0.3269X, \( R^2 = 0.87 \)).

encountered were in the genus *Schizocosa*. Spider capture rates using 16 pitfall traps per block were quite variable among sites [40]. The frequency of spider body length classes over the summer (n = 503 spiders) was: < 7 mm (6 %), 7–15 mm (89 %), and > 15 mm (5 %).

In general, grasshopper nymphs get larger as they develop (Figure 1), with different species often developing at different rates. For the three grasshopper species studied here, individuals are intermediate in size relative to other coexisting grasshopper species. Figure 1 illustrates the range of possible prey sizes that wandering spiders encounter for this set of species based on samples of grasshoppers collected from the field with a sweep net throughout the season. For these grasshoppers, all taxa are about the same size as hatching nymphs; the y-intercept values were not significantly different. On the other hand, *M. sanguinipes* and *P. nebrascensis* reached significantly larger sizes than did *A. deorum*. The slopes of the regression lines differed significantly between *A. deorum* and both *M. sanguinipes* \( (P < 0.03) \) and *P. nebrascensis* \( (P < 0.005) \), but no difference in slope was observed between *M. sanguinipes* and *P. nebrascensis* \( (P = 0.19) \).

2.2. Estimates of stage-specific mortality

Stage-specific mortality was assessed for each developmental stage, beginning with the third instar through the adult stage, each for a 10-d period (the approximate length of a developmental stage) using individuals placed in field cages just as they emerged to that stage. We used two types of wooden-framed (0.25 m² basal area by 0.75 m high) field cages that allowed us to partition mortality due to spider predation from overall, experiment-wise mortality for each developmental stage and species. One cage type (spider predation treatment) allowed naturally wandering spiders to enter and leave while confining grasshoppers (Figure 2A), whereas the other cage type (no spider predation) did not (Figure 2B). Cages permitting spider entry (Figure 2A) were built of fine mesh screen with a 3-mm mesh hardware cloth edge extending 20 cm above the ground along the circumference of the cage; spiders were frequently observed in these cages. The second cage type, both prohibited spider entry and confined grasshoppers (Figure 2B). These cages were built only of fine-mesh screen, allowing no movement of spiders or grasshoppers. No spiders were observed in these fully-screened cages throughout the experiment. Species-specific, stage-based predation by spiders was

![Figure 2. Cage designs used in the spider manipulation treatments. Cages confined grasshoppers that either (A) permitted or (B) excluded spider entry, thus altering risk of spider predation.](image-url)
estimated by comparing the number of surviving grasshoppers from spider enclosures to those in cages which permitted spider entry.

We performed two laboratory experiments to test whether the cages confined grasshoppers while allowing spiders to move freely across the cage boundary. Small replicates (0.10 m² basal area by 0.15 m high) of each cage type were placed in a 20-gallon aquarium, and the movement of individuals followed. In the first experiment, eight individuals from each stage for each grasshopper species were separately placed into each enclosure type. This experiment was replicated four times for all species and developmental stages. Food and water for grasshoppers was placed outside of the enclosure. After 60 h, all third instar and older grasshoppers in both cages were still in both enclosures; instars 1 and 2 were smaller and readily escaped through the hardware cloth mesh. For this reason, the youngest stages could not be evaluated.

The ability of spiders to move through the twoscreen mesh types was also tested in a similar fashion. The goal of the second experiment was to evaluate the efficacy of a semipermeable barrier that allowed spider movement into and out of one cage type (3-mm mesh) but not the other, while always retaining grasshoppers within the cage. Individual spiders were placed into a cage enclosure. To encourage spider movement, we placed 10 grasshoppers and water outside of the enclosure. These treatments were replicated twice for each spider. After 48 h, all spiders (n = 128) with body length less than 15-mm placed within the 3-mm mesh cages moved out, while the fine mesh screen cages kept all spiders confined; spiders > 15 mm could not pass through the 3-mm mesh barrier. Based on natural size-distributions of free-ranging spiders, 95% of the individuals could enter these semipermeable cages.

Eight individuals from one developmental stage for one grasshopper species were placed into each of these two types of cages (with and without spider predation risk) at each block during the natural phenological period of each specific stage for each of the species. Grasshoppers in each cage were censused six times over the 10-d period. The process was repeated for each ensuing developmental stage throughout the field season. After 10 d, all surviving grasshoppers were removed.

For assessing stage-specific mortality rates in the field, cages were arbitrarily placed over patches of similar vegetation at a site, after all spiders and grasshoppers had been removed from the area. Ten replicates (blocks) were established at both grazed (n = 3) and ungrazed locations (n = 7) representative of the area. Locations exhibited a range of naturally occurring grasshopper and spider densities, and a range of vegetation structure. Specific treatments were randomly assigned to cages.

2.3. Experimental design and statistical analyses

Data were analyzed as factorial combinations in a randomized complete block experimental design with 240 cages. With this design, we employed 24 unique treatment combinations of grasshopper developmental instar (4), grasshopper species (3) and spider presence (2), each replicated in 10 blocks. Specific differences in overall mortality rate and the trajectory of 10-d responses to spider predation were assessed by using a repeated measures analysis. However, our experimental design presents an important complication. Since the appearance of grasshopper stages within a species are confounded with season, there is no replication and, hence, no valid comparison for direct comparisons of differences in predation risk by stages (within species). However, seasonal confounding with stage does not preclude comparisons that include stage as part of higher order interactions. As a backup, we also tested the hypothesis that mortality due to spider predation for adjacent stages is equal, using multiple comparisons (Table 1). The effect of cattle grazing regime is not treated as a main effect in the experimental design, but was compared with orthogonal contrast comparisons.

Analyses were performed using Proc GLM [50]. Data were normally distributed and not transformed. Type III sums of squares were used in the analysis to account for missing data from a small number of cages knocked over by grazing cattle in some blocks.

3. RESULTS

3.1. Stage-specific mortality

Earlier grasshopper stages incur higher overall mortality rates from all causes (Table 2, Figure 3), although the effect is not spatially homogeneous (block effect, Table 2). Overall mortality rates averaged over these

| Table 1. Multiple comparisons testing the null hypothesis that mortality due to spider predation between adjacent instars was not different. Only the probabilities associated with pre-planned comparisons are used to protect estimates of the comparison error. An asterisk indicates comparisons that were not performed. |
|-----------------|-----|-----|-----|-----|
|                | 3rd | 4th | 5th | Adult |
| 3rd            |    *| 0.0001|    *|    * |
| 4th            | 0.0001|    *| 0.0041|    * |
| 5th            |    *| 0.0041|    *| 0.0001 |
| Adult          |    *|    *| 0.0001|    * |

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Table II. Repeated measures analysis of variance evaluating the impact of treatments on the number of surviving grasshoppers placed in cages. There is no valid test (NV) for stage as a main effect since it is confounded with seasonal effects as described in Methods. Specific single degree of freedom contrasts for tests of specific hypotheses discussed in the text are also presented.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>Type III SS</th>
<th>Mean square</th>
<th>F</th>
<th>P &gt; F</th>
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<td>541.42</td>
<td>25.79</td>
<td>0.0001</td>
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<tr>
<td>Error_b</td>
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<td>188.96</td>
<td>20.99</td>
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<tr>
<td>Species</td>
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<tr>
<td>Species*spider</td>
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<td>26.86</td>
<td>13.43</td>
<td>1.69</td>
<td>0.19</td>
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<tr>
<td>Species*stage</td>
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<td>154.31</td>
<td>25.72</td>
<td>3.23</td>
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<tr>
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<td>37.84</td>
<td>4.76</td>
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<tr>
<td>Species<em>spider</em>stage</td>
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<td>0.38</td>
<td>0.89</td>
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<td>Error_c</td>
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</tr>
</tbody>
</table>

Orthogonal contrasts include:

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<th>Contrast</th>
<th>df</th>
<th>Sums of square</th>
<th>Mean square</th>
<th>F</th>
<th>P &gt; F</th>
</tr>
</thead>
<tbody>
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<tr>
<td>Spider*stage, adult vs other</td>
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<td>11.25</td>
<td>6.54</td>
<td>0.003</td>
</tr>
<tr>
<td>Grazed vs ungrazed</td>
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<td>7.43</td>
<td>7.43</td>
<td>3.86</td>
<td>0.050</td>
</tr>
</tbody>
</table>

Figure 3. Average number (standard error) of surviving grasshoppers by developmental stage in response to spider treatment for all species combined.

Figure 4. Survival trajectories for grasshoppers under the conditions of these experiments ranged from 91% for 3rd instar nymphs over the 10-d treatment period to about 30% mortality over this time span for adults. Spider predation contributes to mortality in a stage-dependent fashion (spider treatment and spider x stage interaction, Table II, Figure 3). Spider predation contributed proportionally somewhat more to total mortality in 4th and 5th instar nymphs (23.5% of total) compared to 3rd instar nymphs (16% of total), largely because the overall mortality rate of 3rd instar nymphs was much greater. Spider predation exerted no significant mortality on adults for any of these three species (orthogonal contrast, Table II).

Survival trajectories (Figure 4) over the 10-d period for grasshoppers in these comparisons indicate that the effect of spider predation was observed almost immediately (day 1). Trajectories for the two treatments after the first day exhibited similar slopes, suggesting that additional mortality from spider predation was minimal. Repeated-measures multivariate analysis of variance (MANOVA) to test the overall trajectories of mortality indicate that, overall, there were no significant differences in time by spider predation (Wilks’ $\lambda = 0.96$, $df = 5$, $F = 1.2$, $P = 0.30$), species main effect (Wilks’ $\lambda = 0.97$, $df = 10$, $F = 0.45$, $P = 0.86$), spider by species interaction (Wilks’ $\lambda = 0.95$, $df = 10$, $F = 0.76$, $P = 0.67$), spider by grasshopper developmental stage interaction (Wilks’ $\lambda = 0.91$, $df = 15$, $F = 0.12$, $P = 0.44$), species by grasshopper developmental stage interaction (Wilks’ $\lambda = 0.88$, $df = 30$, $P = 0.13$).
3.2. Species-specific selection by predators

Mortality rate from spider predation was similar for all grasshopper species across all developmental stages (species × spider interaction, \( P = 0.19 \); three-way interaction, \( P = 0.89 \)). Contrary to early predictions based on size differences among species at older developmental stages (figure 1), mortality did not differ among developmental stages among grasshopper species (three-way interaction; \( P = 0.9 \)), even though \( A. \) deorum was significantly smaller than the other two species.

3.3. Habitat-specific effects

Vegetation composition and structure contributed to overall mortality as indicated by significant habitat-specific responses. Averaged over all stages and species, mortality was 17% greater in ungrazed locations compared to grazed locations, a significant difference (table II).

4. DISCUSSION

Most predators do not routinely consume prey items in proportion to their abundance, but select a restricted range of sizes and/or stages of prey [15, 39]. Such restricted patterns of predation alter ecological responses in a size-based fashion. For example, life history responses, patterns and dynamics of resource use, or interactions among species are often size-dependent [15, 42, 46, 60]. In addition, size-specific mortality can play a fundamental role in structuring populations and communities of prey [20, 35, 55].

Our main goal aimed at assessing the contribution of spider predation to the mortality of different developmental stages of common grassland grasshoppers, and then describe the overall patterns of risk. We feel that our experimental results accurately reflect the age-specific risk and mortality patterns experienced by free living grasshoppers at the densities we investigated. (i) No other known predators of grasshoppers at this site can pass through the semipermeable cages. As such, we feel that the experiment primarily manipulates predation risk from wandering spiders. This claim is reinforced in that we regularly observed spiders in the semipermeable cages, but never in screen cages during routine censuses. (ii) Foraging decisions reflect natural responses by spiders as influenced by alternate prey. While the experimental cages contained single stages of a single species, the recent foraging experience of wandering spiders entering cages was much broader. As such, foraging spiders made behavioral choices to search in, feed and then leave cages.

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based on recent experience with a wide variety of available prey over the spectrum of sizes available at that time and from a number of patches. (iii) We consciously placed cages at sites with varying grazing history, vegetation structure and plant species composition to obtain as much natural variation as possible for grasshopper and spider densities, species composition as well as for differences in foraging environment to obtain robust estimates. (iv) Finally, experimental densities of grasshoppers, especially those of adults, were on the high end but within the naturally observed range observed at this site since 1978 (Joern, unpublished data). We chose these somewhat high stocking densities to better discriminate among treatments given anticipated high variance among blocks. However, densities were kept within normal ranges of variation so that results could be interpreted with natural conditions in mind. Spider densities, however, occurred at natural densities using this design, and spiders foraged in a normal fashion. Consequently, we feel that the current results can be extrapolated to reasonably reflect naturally occurring processes.

Consistent with expectations, our experiments document that younger (smaller) stages of grasshoppers experienced significantly lower survivorship, a trend that increased in a mostly linear fashion as development stage (and size) increased. Overall, each grasshopper species experienced approximately the same level of stage-specific mortality. Predation from wandering spiders contributed significantly to nymphal mortality, but adults were not affected by this source of mortality. While spider predation was important at all nymphal stages (16–24% of total mortality at each stage could be assigned to spider predation), it is also noteworthy that the majority of stage-dependent mortality reflected other sources. However, the contribution of predation by wandering spiders is likely strong enough that it significantly impacts both the ecological and evolutionary dynamics of these grasshopper species at several levels [2–4, 13, 31, 52].

Lack of a significant difference in mortality rates among grasshopper species suggests that a combined stage- and size-dependent model as opposed to a strictly size-dependent model operated, at least over the size range studied [40]. The significantly smaller A. deorum appears not to have influenced the predator response compared to the other two species, contrary to a strictly size-based rule. Otherwise, A. deorum would be more or less susceptible at later stages (depending on spider foraging rules) because of its smaller size and ready accessibility to most wandering spiders. This was not seen. Specific attributes responsible for such responses were not investigated. However, for the most part, it appeared that size and stage as categories acted in lockstep and provided a good predictor of risk to both overall mortality as well as risk to spider predation.

Field manipulations invariably alter other processes in addition to those targeted. Since our goals were not aimed at specifying underlying foraging rules on the part of wandering spiders, we cannot directly discuss how spiders perceived grasshoppers in cages relative to alternate prey outside of cages. However, we feel that the cage designs are sound for our intended goals, and that the mortality estimates reflect actual processes occurring at natural rates.

4.1. Importance of spider predation to population processes

Stage-dependent risk to predation from spiders was evident and grasshopper densities were significantly depressed for all nymphal stages. Adults were essentially immune to spider predation. Does this mean that spiders are limiting or regulating grasshopper populations at nymphal stages?

Although stage-specific ecological events are taking place at each nymphal stage, understanding the importance of spiders on population processes requires that the impact of predation be integrated over the total life cycle. Because experiments were reset at the beginning of each stage, the impact of previous levels of spider predation on subsequent life stages can not be directly assessed. We also did not investigate the role of density on risk to spider predation or on other sources of mortality by employing a density-series. Initial densities in experimental cages compared to surrounding areas probably represented a quality patch from a spider's viewpoint and facilitated increased foraging effort until grasshopper densities dropped to background levels. As such we can not calculate mortality estimates across stages to assess the contribution of spider predation to grasshopper population dynamics since the densities of later stages reflect earlier density-dependent losses. For population dynamics, the effects are more likely to be multiplicative, and stage-specific survival in this sense must be adjusted for any density-dependent effects. We do not have sufficient data in this study to place our results in this context.

One must understand both total spider predation pressure as well as the mechanisms by which it acts on population dynamics to assess its importance to population dynamics [2]. If stage-specific predation pressure is not too great, compensatory (and depensatory) responses to losses at one stage on the final adult reproductive densities have been routinely documented [3, 12]. In A. deorum [41] and in other grasshopper species [3], moderate but significant losses to spider predation for early and late instar nymphs resulted in the same or slightly higher adult densities, as surviving individuals become seemingly released.
from density-dependent competition for limited food resources. On eliminating spider predation from the system, total mortality rates determining final adult densities may remain the same, but other sources of mortality become important and balance reduced predation rates [11, 12, 41]. As described, underlying mechanisms of spider predation on grasshopper population dynamics can be important even when the overall response at the population level may not be great, but only in the context of the full set of sources of mortality. A basic challenge is to establish the point at which predation promotes either compensatory or depensatory population responses from levels at which spider predation actually contributes to population limitation as a direct factor.

The fact remains that in this study, (i) a significant fraction of nymphs died at each developmental stage, (ii) overall mortality was strongly stage-dependent with the greatest mortality rate falling on younger, smaller individuals, and (iii) significant potential exists for spider predation on grasshopper population processes or other life history attributes. Mechanistic analyses of these relationships must follow to better delineate causal relationships.

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