

Development, growth, and egg production of *Ageneotettix deorum* (Orthoptera: Acrididae) in response to spider predation risk and elevated resource quality

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Abstract. 1. Predation risk to insects is often size- or stage-selective and usually decreases as prey grow. Any factor, such as food quality, that accelerates developmental and growth rates is likely to reduce the period over which prey are susceptible to size-dependent predation.

2. Using field experiments, several hypotheses that assess growth, development, and egg production rates of the rangeland grasshopper *Ageneotettix deorum* (Scudder) were tested in response to combinations of food quality and predation risk from wolf spiders to investigate performance variation manifested through a behaviourally mediated path affecting food ingestion rates.

3. Grasshoppers with nutritionally superior food completed development ≈ 8 –18% faster and grew 15–45% larger in the absence of spiders, in comparison with those subjected to low quality food exposed to spider predators. Growth and development did not differ for grasshoppers feeding on high quality food when predators were present in comparison with lower quality food unimpeded by predators. Responses indicated a compensatory relationship between resource quality and predation risk.

4. Surviving grasshoppers produced fewer eggs compared with individuals not exposed to spiders. Because no differences were found in daily egg production rate regardless of predation treatment, lower egg production was attributed to delayed age of first reproduction. Results compare favourably with responses observed in natural populations.

5. Risk of predation from spiders greatly reduced growth, development, and ultimately egg production. Increased food quality counteracts the impact of predation risk on grasshoppers through compensatory responses, suggesting that bottom-up factors mediate effects of spiders.

Key words. *Ageneotettix deorum*, compensatory interactions, delayed age of first reproduction, grasshopper, Lycosid wolf spiders, predation risk, sandhills grassland, *Schizocosa*.

Introduction

Insects are differentially susceptible to various predators throughout their life cycle, especially as they increase in

size (Price *et al.*, 1980; Sih *et al.*, 1985; McNamara & Houston, 1987; Ludwig & Rowe, 1990). For example, immature grasshoppers are at risk from various predators (Joern & Rudd, 1982; Belovsky *et al.*, 1990; Belovsky & Joern, 1995), most notably spiders (van Hook, 1971; Cherrill & Begon, 1989; Schmitz, 1997; Oedekoven & Joern, 1998, 2000). Predation risk by spiders to immature grasshoppers in grasslands is size or stage-based, where prey eventually escape the threat of

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predation from spiders once they reach a sufficiently large size (usually fifth instar and adult) (Schmitz *et al.*, 1997; Schmitz, 1998; Oedekoven & Joern, 1998, 2000; Okuyama, 1999). In addition to the lethal direct component of predation, spiders may also negatively affect grasshoppers through indirect means by altering the activity budgets of prey, such that defensive and hiding behaviours is increased and foraging decreased, or by restricting access to high-quality, nutrient-rich plant resources (Beckerman *et al.*, 1997; Schmitz *et al.*, 1997; Schmitz, 1998; Oedekoven & Joern, 2000; Danner & Joern, 2003). Ovadia and Schmitz (2002), however, showed that the grasshopper *Melanoplus femurrubrum* responded to the presence of spiders by foraging in alternate microhabitats on less preferred food, with no cost to growth and development. Presumably, *M. femurrubrum* foraging on less preferred food were compensating in some fashion. In either case, grasshoppers potentially forage less efficiently in the presence of spiders, thus reducing nutrient intake necessary for optimal growth, development, survival, and reproduction (Rothley *et al.*, 1997). Negative influences of predators on growth and development have been shown for many prey species from such behavioural modification (Hawkins, 1986; Abrams, 1992; Claus-Walker *et al.*, 1997; McPeck & Peckarsky, 1998; Relyea & Werner, 1999; Morey & Reznick, 2000; Nakaoka, 2000; Peckarsky *et al.*, 2001). This study documents the combined effects of predation by naturally foraging lycosid spiders and elevated plant food quality on the growth, development, and reproduction of the graminivorous grasshopper *Ageneotettix deorum* (Scudder).

Given the relationship between predation risk and foraging efficiency, predator-induced changes of important life history attributes may be manifested in several ways (Houston *et al.*, 1993; Gotthard, 2000; Welton & Houston, 2001; Day *et al.*, 2002). Insect growth and development requires a necessary amount of resources and time to process those nutrients before moulting is possible, bringing with it size increase (Hutchinson *et al.*, 1997). Since both are required to moult successfully, an individual may be able to maintain size by prolonging the duration of development and eating a greater amount of nutritionally poorer food. Another option would be to sacrifice size increase by maintaining developmental rate, assuming foraging rate is altered by predation risk and less food is processed during a given time frame allotted for development, thus leading to decreased size increase (Houston *et al.*, 1993; Hutchinson *et al.*, 1997). Alternately, both individual growth and developmental rate could be negatively impacted through this behaviourally mediated trade-off if foraging and maintenance schedules are both altered sufficiently. All these scenarios may then subsequently affect reproductive dynamics in some manner during the adult life cycle stage (Houston & McNamara, 1990; Welton & Houston, 2001; Day *et al.*, 2002; Branson, 2003).

Since susceptibility of *A. deorum* to predation from spiders is size-based, increased nymphal growth and accelerated developmental rate will release grasshoppers from susceptibility to predators sooner (Oedekoven & Joern, 1998). Increased acquisition rate of nutritionally high qual-

ity plant material facilitates accelerated individual development (Johnson & Mundel, 1987; Yang & Joern, 1994a, b; Joern & Behmer, 1997), decreasing exposure time to an important source of mortality. In many cases, high quality food is spatially distributed such that exposure to predators is increased during grasshopper foraging activity (Joern & Lawlor, 1980; Schmitz, 1998; Sokol-Hessner & Schmitz, 2002). Alternately, grasshoppers with a broader diet can avoid predation risk by foraging on suitable, less preferred plants in microhabitats that provide more cover and thus decrease detection by spiders. This shift may incur a cost of reduced nutritional quality of alternate food types (Schmitz *et al.*, 1997; Schmitz, 1998; Ovadia & Schmitz, 2002); reduced risk of mortality from a predator may allow the grasshopper to maintain regular individual growth and development rates, as was found for *M. femurrubrum* (Ovadia & Schmitz, 2002). Many insect herbivores, however, such as *A. deorum* have restricted diets and cannot switch to alternative food sources; less time spent foraging reduces the final nutritional budget, which in turn influences the reproductive dynamics of grasshoppers either by (a) reducing food reserves gained from nymphal feeding that are later allocated to egg production, or by (b) delaying the timing of first reproduction and thus reducing total lifetime reproductive effort, all else equal.

Given the importance of high food quality and predator avoidance to successful growth and development, it is hypothesised that these factors will act synergistically to affect the performance of immature grasshoppers (Joern & Gaines, 1990; Belovsky & Joern, 1995; Schmitz, 1998; Ovadia & Schmitz, 2002). It was predicted that growth and developmental responses under conditions of high predation risk and enriched food quality would not differ significantly from the combination of ambient resource quality and predator absence. That is, high food quality offsets the harmful effects resulting from the presence of predators. Altered developmental rate mediated through predation risk's alteration of foraging efficiency (Beckerman *et al.*, 1997; Schmitz *et al.*, 1997; Schmitz, 1998; Ovadia & Schmitz, 2002; Danner, 2002) may affect the reproductive efficiency of adults. Grasshoppers often have only a limited window of time in which to reproduce before the end of the growing season, a period that often ends suddenly from the lack of sufficient quality food or extreme temperatures in North American grasslands (Joern, 1982; Belovsky & Joern, 1995). Early reproduction is imperative in these cases.

Using field experiments, the developmental, growth, and reproductive responses by *A. deorum* to combinations of spider predation and host plant quality were investigated. *Ageneotettix deorum*, a common grasshopper found in grasslands throughout central North America, is strictly graminivorous and primarily eats grasses in the genus *Bouteloua* (Joern, 1985). Under conditions of high resource quality and no spider predators, it was predicted that grasshoppers would experience the highest rate of development and achieve larger final adult size. It was expected that lower resource quality coupled with risk of predation would prolong the duration of development and result in

smaller surviving grasshoppers as adults. It was also hypothesised diminished reproduction in comparison to other treatment combinations for grasshoppers completing development and surviving to maturity while exposed to predators.

Methods and materials

Study site

Field experiments were conducted during the summers of 2001 and 2002 at Arapaho Prairie, a research 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 includes vegetation characteristic of both short and tallgrass prairie (Joern, 1985). Approximately 200 plant species occur on site, of which 80% are forb species. Roughly 80% of the biomass and structure of vegetation is composed of grasses (Keeler *et al.*, 1980; Barnes & Harrison, 1982). Overall, adult grasshopper densities at Arapaho Prairie average 4–5 individuals/m² in most years (Joern & Pruess, 1986; A. Joern, unpubl. data). *Ageneotettix deorum* occurs at relatively high densities, averaging 1–2 adults/m² (Joern & Pruess, 1986; A. Joern, unpubl. data), and immature density approached 30 individuals/m² in some habitats during this study (Danner, 2002).

The most common grasshopper predators and parasitoids found in this system are spiders, insects (most notably Diptera: Asilidae, Tachinidae, and Sarcophagidae), and birds (primarily grasshopper sparrows and western meadowlarks) (Joern & Rudd, 1982; Joern, 1988, 1992; Oedekoven & Joern, 1998). At this site, birds feed on adults (Joern, 1986, 1988, 1992; Kaspari & Joern, 1993), while immature grasshoppers are most susceptible to spider predation (Oedekoven & Joern, 1998). All grasshopper nymphs used in this experiment were collected from Arapaho Prairie and nearby areas using sweep nets.

Weather is quite variable at this site. The 15-year mean cumulative precipitation collected from an on-site weather station during the experimental period, 1 June to 15 August, was 14.9 ± 1.7 cm. In 2001, accumulated rainfall during this period was 17.2 cm, slightly above normal. In 2002, only 11.6 cm of rain fell over the summer period, and 52% of this precipitation fell over a 12-h period during the first week of July. Foliar nitrogen concentration in non-fertilised plants increased 10% in 2002 relative to 2001 (Danner, 2002).

Cage design

Grasshoppers were contained in field cages (0.66 m wide × 0.66 m deep × 0.80 m tall; ≈0.40 m² basal area) similar to those described by Oedekoven and Joern (1998, 2000). After removing all grasshoppers, spiders, and other detectable arthropods from the area, cages were buried 20 cm into the ground over suitable natural vegetation

composed primarily of *Bouteloua gracilis*. Cages were designed to extend well above grass canopy height during experiments. Prior to stocking experimental grasshoppers, all cages were checked and any unintentional residents were removed. All four sides and lids of half the cages were fully covered with insect screening with a mesh size of less than 1 mm. The remaining cages were constructed as above, with the substitution of a 3-mm mesh, 10 cm tall strip of hardware cloth along the ground. Using this mesh size successfully retains experimental grasshoppers, yet allows entry by softer bodied spiders, as documented by Oedekoven and Joern (1998). Twenty cages of each type were constructed (10 replicates of each treatment per year). To document that wolf spiders actually moved into cages with hardware cloth screen, Tanglefoot[®] was applied to 4 cm wide wooden strips placed along a random side of the cages prior to and after the experiment. Spiders were captured in all traps, both before and after the experiment, indicating active spider foraging behaviour throughout the experiment. In addition to Tanglefoot[®] traps, wolf spiders were observed in all cages designed to allow their entry, and none in the others; however, it was not possible to keep accurate records of spider density within experimental cages during census.

Experimental conditions

Predators and food quality were manipulated in a 2 × 2 factorial, randomised complete block experiment, with treatment combinations randomly assigned to cages within each block. Different levels of food quality were established by applying an aqueous solution of Miracle Gro[®] N–P–K (15–30–15) plant fertiliser at a concentration of 7.5 g N/m². Vegetation in low food quality cages (unfertilised natural vegetation) was treated with an equivalent amount of water only. A 230-cm² sample of above-ground biomass from each of the 40 cages was clipped, dried, weighed, and analysed for foliar nitrogen content both prior to and after the experiment. Nitrogen content of plant tissues was elevated throughout the experiment in response to the fertiliser treatment in both years of the experiment (Danner, 2002). Cages were stocked with 20 fourth-instar grasshoppers, which was about twice natural field densities (≈23 per m² in 2002) at the time (Danner, 2002), but well within the range of naturally occurring densities during some years (Joern & Pruess, 1986; A. Joern, unpubl. data).

Grasshopper performance

Developmental rate and growth were recorded for all surviving grasshoppers. Developmental progression of immature grasshoppers was based on wing pad development (Scoggin & Brusven, 1972), and developmental rate was measured as the length of time required to complete two moults. The length of the right metathoracic femur was used to measure individual growth. Femur length adequately characterises grasshopper size (Cueva del Castillo *et al.*,

1999) and is readily measured in the field. All grasshoppers detected within a cage were measured at each census in order to obtain a reliable estimate of growth over time. Survival was tracked every 2–4 days over the experiment's duration. In 2001, cages were stocked during the first week of July, and in 2002, cages were stocked the second week of June. Experiments were stopped after the first 2 weeks of August in both years.

At the conclusion of the experiment, all surviving females were collected, immediately frozen, and ovaries later dissected to estimate reproductive performance. In 2001, females were collected 2 weeks after all grasshoppers had become reproductively active. In 2002, the period for reproduction was extended to 4 weeks before ending the experiment to better resolve differences in egg production among treatment combinations. Ovariole analysis followed standard techniques (Phipps, 1949, 1966; Launois-Luong, 1978; Branson, 2003). Ovaries were dissected in insect saline (7.5 g NaCl/l solution) and egg production and resorption assessed using a dissecting microscope (60–500× magnification). When an egg is successfully produced and transported to the oviduct for laying, a thin, reddish-brown remnant (termed follicular relict) is deposited on the ovariole pedicel that can be scored readily (Launois-Luong, 1978). β -carotene pigmented bodies (resorption bodies) were also found in the pedicels of ovarioles. Resorption is a process in which resources in a developing oocyte are reincorporated for other needs or diverted to the successful production of another viable egg, leaving the resorption body in the process (Phipps, 1966; Launois-Luong, 1978; Branson, in press). Counting the number of functional ovarioles, follicular relicts, and resorption bodies allowed the number of egg pods and the total number of eggs produced to be estimated.

To estimate naturally occurring reproductive dynamics of free-ranging *A. deorum* for comparison with experimental results, a natural population was censused at weekly intervals in 2002 according to Onsager and Henry (1977) until very few *A. deorum* remained. Initially, adult grasshoppers were detected the first week of July (Danner, 2002). To evaluate egg production rates in natural populations, 10 individuals were collected and dissected each week from 14 July until 19 August 2002, at which time it was only possible to collect four females in an hour of intense collecting effort, a point that corresponded to very low numbers in independent density estimates of the natural population.

Using sampling methodology outlined by Onsager and Henry (1977), 25 0.1 m² rings were placed randomly along four 100-m transects, no closer than 2 m from each other. Total grasshopper density was estimated by counting the number of individuals in each sampling ring on sunny days when wind speed was less than 10 mph and air temperature was greater than 25 °C. Relative abundance of *A. deorum* was estimated as the number of *A. deorum* in samples in relation to other grasshoppers collected in sweep net samples; approximately 50 sweeps per transect were taken for each sampling date. *Ageneotettix deorum* density was determined by multiplying relative abundance by total grasshopper density.

Statistical analyses

ANCOVA was used to assess differences in development rate of the immature grasshoppers; the proportion of stocked individuals still alive at the time of the final moult was used as the covariate (Sokal & Rohlf, 1981). Growth of the hind femur was analysed using repeated-measures ANCOVA; the proportion surviving to complete the final moult again used as the covariate. Tests for homogeneous slopes in ANCOVA were conducted (SAS Online Doc, V8; SAS Institute, 1989), resulting in non-significant differences ($P > 0.53$). A summary of treatment cage densities is provided in Table 1. All specific treatment comparisons were evaluated using a Tukey's adjustment to avoid increasing Type I errors given the large number of planned comparisons (Kuehl, 2000). Growth was also estimated as the total increase in femur length averaged per cage, analysed with ANCOVA, with survivorship as a covariate. Reproductive activity, measured as the number of follicular relicts and resorption bodies, was analysed using a non-parametric Wilcoxon two-sample test to compare between predation exposure and fertilisation treatments. A non-parametric test was used in this instance because many of the experimental grasshoppers died before the experiment was concluded (Table 1), reducing the sample size. Because of significant differences in weather between years, analyses were conducted separately for each year. Data were normalised using a log transformation when necessary (Sokal & Rohlf, 1981). All analyses were conducted using SAS/STAT.

Results

Development and growth

Effects of treatment combinations on developmental rate are shown in Fig. 1a. Development of grasshoppers in

Table 1. Mean (± 1 SE) grasshopper densities per caged treatments. Adult/pre-reproductive densities were calculated using densities once all survivors in a cage had completed the final moult. The final densities were calculated using the last observed number of survivors on the final day of the experiment, in both years. All surviving females counted in this final census were collected, frozen, and dissected to determine reproductive dynamics.

Treatment	Cage density (grasshoppers/cage)	
	Adult/Pre-reproductive	Final census
<i>2001</i>		
F+/NP	9.4 (1.6)	4.2 (1.2)
F+/P+	6.3 (1.3)	2.1 (1.4)
NF/NP	10.3 (0.7)	5.2 (1.3)
NF/P+	11.8 (1.7)	3.9 (3.3)
<i>2002</i>		
F+/NP	9.2 (0.4)	3.1 (1.3)
F+/P+	6.9 (0.3)	2.4 (0.9)
NF/NP	7.6 (0.5)	1.3 (0.9)
NF/P+	6.7 (0.6)	3.6 (2.5)

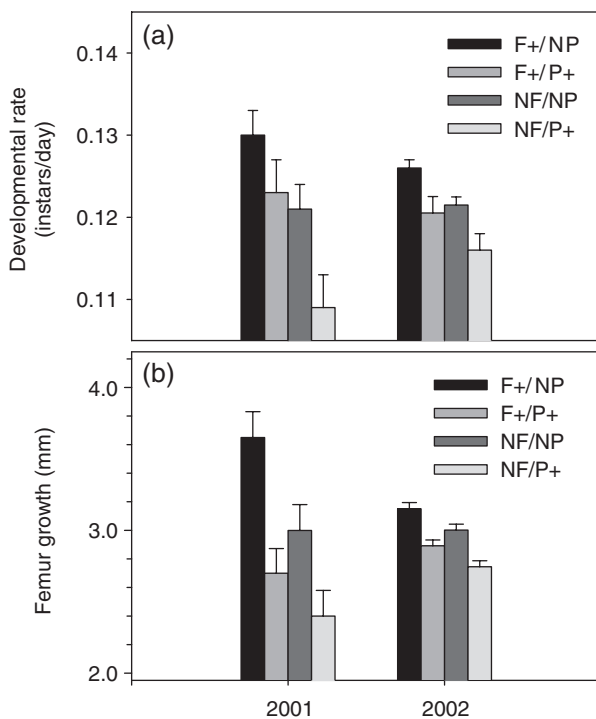


Fig. 1. (a) Mean developmental rate of individual grasshoppers that survived to adulthood (mean \pm 1 SE) for fertiliser [fertiliser addition (F+), no fertiliser (NF)] and predation [predator entry (P+), predators restricted (NP)] treatment combinations. In both years of the experiment, high resource quality coupled with predator exclusion accelerated development, while ambient predation risk and low food quality caused reduced developmental rate. All treatments were compared, within year only, with a Tukey's adjustment. (b) Growth of the hind femur (mean \pm 1 SE) of grasshoppers that completed development for fertiliser and predation treatment combinations. Maximum growth was attained under conditions of elevated resource quality and predator absence in both years, while non-fertilised vegetation and ambient predation resulted in smaller adult size. All treatments were compared, within year only, with a Tukey's adjustment.

response to increased total nitrogen content of host plants was accelerated in both years (2001: $F_{1,23} = 26.35$, $P < 0.01$; 2002: $F_{1,26} = 9.97$, $P < 0.01$). Exposure to ambient levels of lycosid spider predation prolonged nymphal development (2001: $F_{1,23} = 13.16$, $P < 0.01$; 2002: $F_{1,26} = 19.47$, $P < 0.01$). Although developmental rate responded to both spider predation and host plant quality, there was no significant interaction between the two treatments (2001: $F_{1,23} = 0.04$, $P = 0.85$; 2002: $F_{1,26} = 0.12$, $P = 0.73$; Fig. 1a). No significant difference was observed in rate of development between fertilised/predation compared to no-fertiliser/no-predation treatments combinations in either year (Fig. 1a). In 2001, grasshoppers completed development of the last two nymphal stages approximately 26.9% faster when food plants were fertilised and predators were absent than when food plants were of lower quality with spiders present. In 2002, the acceleration of development was approximately

9.3% faster for the same treatment conditions in a generally drier year.

Increased nutritional quality of host plants and absence of spider predators significantly enhanced the growth of immature grasshoppers in both years (Fig. 1b, Table 2). Hind femur lengths of adults eating high quality vegetation in the absence of spider predators were approximately 45% greater than those feeding on lower quality conditions with the risk of predation ($F_{1,23} = 42.12$, $P < 0.01$) in 2001 and 15% larger in 2002 (Fig. 1b; $F_{1,26} = 36.35$, $P < 0.01$). No differences were detected for mean hind femur growth of grasshoppers for the fertilised/predation vs. no-fertiliser/no-predation treatment combinations for either year (Fig. 1b).

Reproduction

No significant differences in the number of egg pods produced in response to predation risk were found (Table 3), but fewer follicular relicts were produced in the presence of spiders (Fig. 2a). Egg production rate, measured as follicular relicts (2001: $Z = 0.19$, $P = 0.42$; 2002: $Z = 0.41$, $P = 0.13$) and resorption bodies (2001: $Z = 0.05$, $P = 0.48$; 2002: $Z = 0.17$, $P = 0.43$), did not respond significantly to host plant quality in either year, contrary to expectations. Exposure to spider predators marginally reduced the production of follicular relicts and increased egg resorption (Table 3). In 2001, grasshoppers produced almost twice as many follicular relicts during the first 2 weeks as a reproductively active adult when not exposed to spider predators ($Z = 1.54$, $P = 0.06$; Fig. 2a), a marginally significant result. No differences were detected in the number of egg resorption bodies ($Z = 0.01$, $P = 0.50$). In 2002, approximately 22% more follicular relicts were detected when spiders were absent ($Z = 1.45$, $P = 0.07$; Fig. 2a). There was also a statistically marginal increase in egg resorption when grasshoppers were exposed to spiders ($Z = 1.64$, $P = 0.05$). Under conditions of predation risk, grasshoppers resorbed approximately 35% more eggs than when predators were absent (Table 3).

Two hypotheses may explain these results: reduced allocation of resources to egg production or delayed onset of reproduction. To resolve this, the number of follicular relicts produced per day since the time each grasshopper completed its final moult were calculated. No differences were found in daily egg production rate in response to spider predation risk in either year of the experiment (Fig. 2b) (2001: $Z = 0.69$, $P = 0.25$; 2002: $Z = 0.80$, $P = 0.21$). The alternate explanation is that an observed difference in total egg production is due to delayed onset of reproduction. This result becomes crucial when one considers the abruptness at which grasshopper populations can crash in the end of the summer growing season, as was documented in 2002. A steady increase in egg production was found over the approximately month-long period of sample (Fig. 3), until an abrupt population decline in the middle of August (Figs 3 and 4).

Table 2. Repeated measures ANCOVA for the growth of the hind femur of immature grasshoppers that survived to become adults. The number of grasshoppers per cage at the time of the final moult was used as a covariate. Significant interactions between time and main effects represent the variable effect of these treatments over the temporal development of grasshoppers. Predation risk exerted a negative effect and fertilised vegetation exerted the greatest positive effect early during the experiment. As the experiment progressed, the effects of both tapered off given decreasing susceptibility to spider predation and depletion of plant material over time.

Source	d.f.	F	P	d.f.	F	P
<i>Between subjects</i>						
<i>2001</i>						
Block (B)	9,23	0.55	0.824	9,26	0.88	0.554
Fertiliser (F)	1,23	19.70	<0.001	1,26	125.73	<0.001
Predation (P)	1,23	70.79	<0.001	1,26	81.90	<0.001
F × P	1,23	1.42	0.245	1,26	0.01	0.929
Survivors/cage	1,23	0.18	0.677	1,26	5.91	0.022
<i>Within subjects</i>						
<i>2002</i>						
Time (T)	3,69	42.75	<0.001	7,182	163.53	<0.001
T × B	27,69	0.95	0.539	63,182	1.03	0.435
T × F	3,69	7.52	0.002	7,182	10.24	<0.001
T × P	3,69	13.69	<0.001	7,182	9.62	<0.001
T × F × P	3,69	2.18	0.118	7,182	0.55	0.796
T × Survivors/cage	3,69	0.60	0.615	7,182	1.32	0.243

Discussion

Evaluating performance trade-offs of prey searching for food in the presence of predators is a central problem in behavioural and community ecology, one made more challenging when indirect, and trait-mediated responses operate (McNamara & Houston, 1987; Lima & Dill, 1990; Ludwig & Rowe, 1990; Stamp & Bowers, 1993; Wootton, 1994; McPeck & Peckarsky, 1998; Nakaoka, 2000). This study is motivated by such behaviourally mediated effects, where the presence of spiders reduces the time grasshoppers are able to forage (Danner & Joern, 2003), thus changing the dynamics of how each parcel of food is valued and allocated

to the primary life history attributes of growth, development, and reproduction.

Nymphal performance

Hind femur growth and developmental rates responded to food quality and natural levels of predation risk in a non-linear fashion. As predicted, the comparison of *no spiders/high food quality vs. ambient spider predation/low quality food* resulted in the largest difference in both growth and development (Fig. 1a,b). No significant difference in growth or developmental rate was also found between

Table 3. Mean (± 1 SE) femur length and reproductive effort of female survivors per fertiliser (F+, NF) and predation risk (P+, NP) treatment combinations. Clutches produced was estimated by dividing the number of resorption bodies and follicular relicts by the number of fully developed ovaries. The mean number of eggs per clutch per treatment was calculated for grasshoppers able to produce at least one clutch. The reduced number of successful clutches oviposited and the size of those clutches among predator treatments is further evidence of delayed reproduction, most likely in response to slowed immature development.

Treatment	Survivors	Femur	Relicts	Reproductive effort		
				Resorbed	Clutches	Mean clutch size
<i>2001</i>						
F+/NP	15	9.88 (0.22)	1.33 (0.47)	2.33 (0.56)	0.67 (0.11)	2.86 (0.93)
F+/P+	6	9.30 (0.22)	1.67 (0.92)	2.17 (0.83)	0.47 (0.07)	2.50 (2.83)
NF/NP	28	9.14 (0.12)	2.18 (0.47)	2.39 (0.24)	0.64 (0.06)	3.26 (0.47)
NF/P+	18	9.58 (0.08)	0.89 (0.35)	2.72 (0.30)	0.33 (0.06)	2.67 (0.76)
<i>2002</i>						
F+/NP	9	9.74 (0.19)	7.78 (1.51)	2.11 (0.72)	1.88 (0.15)	4.52 (0.25)
F+/P+	8	9.69 (0.23)	7.63 (0.80)	2.63 (0.63)	1.58 (0.15)	4.17 (0.31)
NF/NP	8	9.49 (0.18)	8.13 (0.64)	2.00 (0.27)	1.88 (0.04)	4.31 (0.05)
NF/P+	13	9.38 (0.16)	5.46 (0.77)	2.92 (0.37)	1.43 (0.15)	3.50 (0.16)

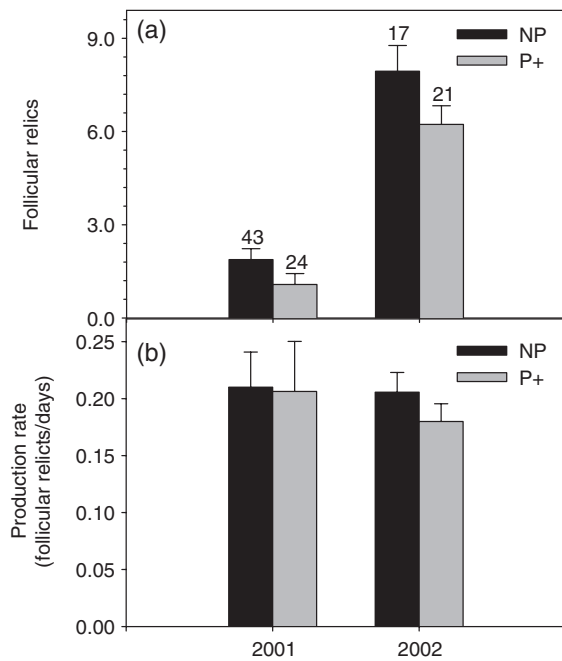


Fig. 2. Reproduction in response to predation treatments. Values are means \pm 1 SE. (a) Average follicular relicts counted for females surviving to the end of the experiment in response to ambient predation. The number of survivors per treatment is given. During both years of the experiment, grasshoppers in cages that allowed the migration of spider predators produced a significantly reduced number of follicular relicts, or viable eggs. (b) Production of eggs by females who successfully produced at least one clutch before dying from the time since the final moult occurred. No differences were detected between the maturation rates of viable eggs between predation treatments in either year. Although differences were detected in production of follicular relicts in response to ambient predation (Fig. 3), the equivalent production rates between the treatments suggest the basis for that response is a delay in reproductive capability due to prolonged nymphal development in the presence of ambient spider predation.

high predation risk/high food quality compared with no predators/low food quality (Fig. 1a,b). Collectively, these results indicate that both food quality and predation are important, and that high quality diet can compensate for the negative effects of indirect spider predation risk (*sensu* Oedekoven & Joern, 2000).

Reduced feeding by *A. deorum* in the presence of spiders provides a behavioural mechanism to explain these results. In a related study, immature *A. deorum* spent about 50% less time walking, an important component of foraging for quality food, and several orders of magnitude less time actually feeding in the presence of spiders (Danner & Joern, 2003). Decreased time spent feeding reduces the amount of food eaten in grasshoppers (Rothley *et al.*, 1997). Indirect effects of spiders on feeding were not observed for fifth instar nymphs and adults, indicating that indirect impacts caused by spiders occur early in the life cycle.

The elapsed time required for a grasshopper to complete development and reach adult size is important in the face of

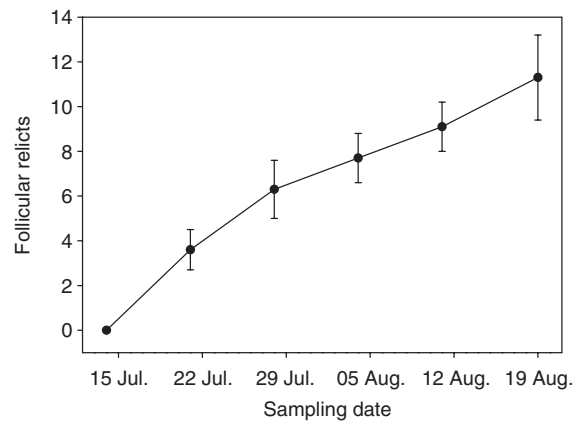


Fig. 3. Mean (\pm 1 SE) number of follicular relicts produced by sampled free-ranging females in 2002. All points represent a sample size of $n = 10$, except for the point on 19 August, where it was only possible to capture four grasshoppers within a 1-h period. Naturally occurring densities of *Ageneotettix deorum* past mid-August were extremely low, suggesting this grasshoppers' limited time to effectively reproduce.

size-selective predation risk from spiders (Oedekoven & Joern, 1998; Schmitz, 1998; Danner, 2002). Success for spiders preying on grasshoppers declines as prey get larger because they cannot successfully attack large nymphs and adults. Because of this, factors that promote faster growth will be beneficial. It was observed that increased developmental and growth rates resulted when *A. deorum* was provided with higher quality food. These results are in line with results from studies of other organisms (Werner *et al.*, 1983; Sih *et al.*, 1985; Abrahams & Dill, 1989; Huang & Sih, 1990; Skelly & Werner, 1990; Feltmate & Williams, 1991; Schmitz, 1994; Anholt & Werner, 1995; Walde, 1995).

These results contrast somewhat with those of Ovadia and Schmitz (2002) who found that spider predation risk

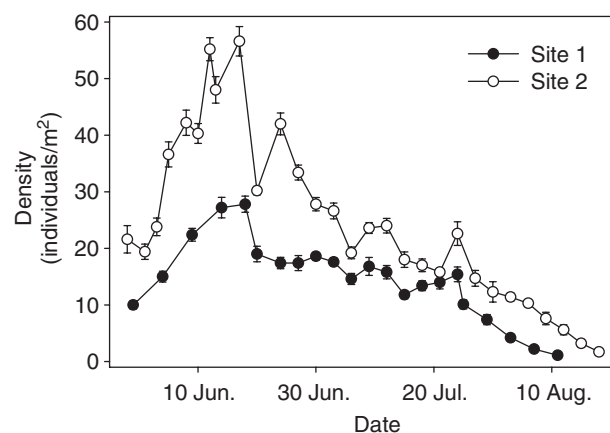


Fig. 4. Changes in densities of natural *Ageneotettix deorum* populations at two sites in 2002. Site 1 represents grassland adjacent to field experiments. Site 2 represents grassland approximately 50 km south. Values are means \pm 1 SE.

did not affect the growth and development in the grasshopper *M. femurrubrum*. Combined, results of these two studies provide a comprehensive picture of the influence of foraging–predation risk trade-off in grasshoppers based on the same underlying theme. A primary difference between *M. femurrubrum* and *A. deorum* is the ability of individual grasshoppers to find safe microhabitats in which to forage and still obtain at least minimal quality food. As a group, grasshoppers display a wide variety of feeding behaviours and a range of diet preferences (Mulkern *et al.*, 1969; Joern & Lawlor, 1980; Joern, 1985; Schmitz, 1994). *Ageneotettix deorum* is an obligate grass-feeder with a narrow diet breadth, and primarily feeds on two *Bouteloua* (grama grass) species found in the same microhabitat (Joern, 1985). Alternately, *M. femurrubrum* feeds on a variety of both grasses and forbs from different microhabitats. In the absence of predation risk, *M. femurrubrum* prefers grasses, but switches to foraging on forbs in a habitat that provides a partial refuge to predation when spiders are present (Ovadia & Schmitz, 2002). On forbs, *M. femurrubrum* can continue foraging and maintain nutritional input sufficient to meet needs above that possible if no refuge was available. Consequently, growth and development of *M. femurrubrum* was less affected by predation risk than was observed for *A. deorum*, which does not alternate between foraging habitats. Reduced developmental rate during immature stages of *A. deorum* in this study resulted from the effect caused by predation risk from spiders in reducing feeding rates coupled to the absence of alternative food sources. When plants are fertilised, however, individuals can compensate for reduced intake because they obtain higher quality food in less time spent feeding, so that there is no significant reduction in growth or development. This result further substantiates the conclusion that food is important in mediating this interaction.

Reproductive performance

Foraging interference from predation risk to immature grasshoppers subsequently affected egg production during the adult stage as well. It was predicted that egg production would be greater in fertilised plant treatments (Phipps, 1949, 1966; Sanchez *et al.*, 1988). In controlled laboratory feeding studies, egg production in *A. deorum* was highest when fed diets with $\approx 25\%$ protein (Joern & Behmer, 1997). In this field experiment, it was found that availability of previously fertilised host plants did not result in an increased number of follicular relicts or a decreased number of resorption bodies (Table 3). Egg resorption between years among equivalent treatments was highly consistent, even when environmental conditions were quite different (Table 3). In August, *Bouteloua* contains between 6 and 10% protein in both fertilised and unfertilised treatments, levels that are well below those needed to support the high egg production rates seen in lab feeding studies. Furthermore, Branson (2003) has shown that egg production in the grasshopper *Melanoplus sanguinipes* does not depend on

nutrients acquired during nymphal stages, but only on those obtained as adults. It appears that food quality is too low during the peak reproductive period to support high reproductive rates.

Reproductive output decreased in response to exposure to spider predators (Table 3, Fig. 2a), but no difference in egg production per day since becoming an adult was found between predator vs. no predator treatments (Fig. 2b). This suggests that delayed development caused by effects from predation risk on nymphs (Fig. 1a) is the basis for the observed decline in egg production (Fig. 2a).

This raises the critical issue of whether these results and interpretations are relevant for understanding natural populations. In the experiment, all treatments were ended at the same time in mid-August, in part to assure that there would be enough surviving females for dissection. Would such a sudden end to the season be typical for this species, and would it typically be this early? The answer is yes to both issues. Naturally occurring *population crashes* in *A. deorum* in late summer are common at this site, naturally truncating population abundances. This suggests that the experimental protocol mimics natural conditions reasonably well. In a natural population of *A. deorum*, production of follicular relicts increased linearly over time, from mid-July to mid-August (Fig. 3), the period of this experiment. Note that it was not possible to find many females for dissection on the last date of the sample in mid-August (19 August 2002, Fig. 3); only four females were found in an hour searching time, where previously 10 females had been caught in 5–10 min. The search was carried out over a large enough area so that this decline is not simply the result of previous collections. Additional evidence also documents that free-ranging populations of *A. deorum* declined precipitously beginning in early August (Fig. 4). This decline was widespread in extent, and again suggests that a limited window of reproductive opportunity generally exists for *A. deorum* individuals who reach adulthood. Based on the organism's natural history, it is argued that susceptibility to spider predation as a nymph likely reduces potential reproductive output by delaying the onset of first reproduction. Because individuals from all treatment combinations have the same daily egg production rate, the number of days available for reproduction becomes the critical attribute. Because of the sudden end to the season, delayed age of first reproduction thus reduces lifetime egg production in *A. deorum*.

Conclusions and general significance

As seen in this study, lycosid spiders have the potential to affect the growth, development, and egg production of *A. deorum* indirectly by reducing foraging rates and acquisition of resources. There has been considerable dispute about whether top-down (Beckerman *et al.*, 1997; Schmitz *et al.*, 1997; Letourneau & Dyer, 1998; Moran & Hurd, 1998; Halaj & Wise, 2001) or bottom-up processes (Forkner & Hunter,

2000; Schmitz *et al.*, 2000) are most important for controlling insect herbivores. Both often contribute. As observed in this study and others, behaviourally mediated responses by insect herbivores (Denno *et al.*, 2002; Finke & Denno, 2002; Ovadia & Schmitz, 2002) or predators (Losey & Denno, 1998, 1999; Rosenheim, 1998; Okuyama, 1999) can also be very important. Altered foraging behaviour in the presence of spiders results in important changes in life history attributes. Moreover, it was observed that increased food plant quality has the potential to override negative effects resulting from predation risk in a compensatory manner, indicating that bottom-up forces can effectively mediate effects of natural enemies (Botrell *et al.*, 1998; Oedekoven & Joern, 2000; Denno *et al.*, 2002). Although increased resource quality may ameliorate negative influences imposed by indirect risk of spider predation during immature stages (Price *et al.*, 1980; Leibold, 1989; Rothley *et al.*, 1997; Schmitz *et al.*, 1997; Oedekoven & Joern, 1998, 2000; Schmitz, 1998; Danner, 2002), direct and indirect effects of predation risk combined have the potential to affect the lifetime fitness of this grasshopper.

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