

## Life-history Responses of *Ageneotettix deorum* (Scudder) (Orthoptera: Acrididae) to Host Plant Availability and Population Density

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**ABSTRACT:** The effects of variation in host plant availability and population densities on reproductive allocation in grasshoppers have received relatively little attention. The effect of increased host plant availability and population density on survival and reproductive allocation were examined in a widely distributed grasshopper, *Ageneotettix deorum* (Scudder). The experimental treatments consisted of ambient-level and fertilized vegetation with two *A. deorum* density treatments in a 2 × 2 factorial design. Both food plant availability and population density played important roles in the observed life history variation. Although the rate of egg pod production was not density-dependent, density-dependence was evident in the number of eggs per pod. Average survival did not respond to food plant availability, but reproduction was limited by host plant availability in the ambient-level treatment. Food limited *A. deorum* with ambient-level resources produced egg pods more slowly and with fewer eggs per pod. The rate of egg pod production averaged 64% higher with fertilized vegetation than with ambient vegetation. The availability of higher protein host plants may have been the primary limiting factor for egg production. The effects of food availability and grasshopper density acted in an additive manner on reproductive allocation. As a result, the *per capita* availability of nutrients was likely the limiting factor for reproduction in both resource and density treatments. Variation in host plant availability had a much larger effect on recruitment and population dynamics than would be predicted based on survivorship alone.

**KEY WORDS:** Acrididae, reproductive allocation, host plant availability, fecundity, grasshopper

The quality and abundance of host plants available for grasshoppers varies in relation to yearly climate conditions. Although host plants often appear abundant in the environment, host plant quality varies greatly within and among plants and within years (Joern and Behmer, 1997). Grasshoppers (Orthoptera: Acrididae) appear capable of adaptive modifications in resource allocation (de Souza Santos and Begon, 1987; Branson, 2003a) and exhibit demographic responses to changes in host plant quality and availability (Branson, 2003b; Joern and Behmer, 1997, 1998; Joern, 2000; Danner and Joern, 2004). Despite considerable research on the effects of competition and resource enhancement on nymphal and adult grasshopper survival (Joern and Klucas, 1993; Belovsky and Slade, 1995), the effects these factors have on reproductive allocation have received relatively little attention (Branson, 2003a, b; Danner and Joern, 2004). The effects of population density on reproduction and survival of North American grasshoppers typically occur through exploitative competition for host plants (Joern and Klucas, 1993; Belovsky and Slade, 1995; Branson, 2003b). Declining per capita availability of high quality food with increasing population densities led to reduced survival and reproductive allocation in *Melanoplus sanguinipes* (Fabricius) (Acrididae) (Branson, 2003b). Past research has led to little predictive power about how variability in resource availability and population density affects reproductive allocation and population dynamics of grasshoppers (Joern, 2000).

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Grasshoppers have determinate growth and only allocate significant resources to reproduction as adults (Branson, 2004). Grasshopper ovaries consist of a series of ovarian follicles which are typically not all functional under often resource-limited field conditions (Bellinger *et al.*, 1987; Joern and Gaines, 1990; Branson, 2003a, b, 2004). Grasshoppers can reduce allocation to reproduction when resources are limiting by reducing vitellogenesis or increasing oosorption (Chapman, 1998), presumably allocating a higher percentage of available resources to maintenance, resulting in higher survival (Papaj, 2000). Vitellogenesis occurs when the ovarian follicle initiates development and appears largely controlled by adult experience (Chapman, 1998). Reduced reproductive allocation can also occur by oosorption, or resorption, of developing ovarian follicles (Joern and Klucas, 1993), which results in a brightly colored band called a resorption body.

*Ageneotettix deorum* is a widely distributed univoltine Gomphocerine grasshopper that is often a dominant species in grasshopper outbreaks (Pfadt, 2002). It is primarily graminivorous, feeding on several common grasses and sedges (Mulkern, 1967; Pfadt and Lavigne, 1982). In controlled laboratory experiments, egg production positively responded to increased nitrogen levels in diets (Joern and Behmer, 1997). *Ageneotettix deorum* lays small egg pods of up to 6 eggs, typically in the top 0.6 cm of soil (Shotwell, 1941), which allows recovery of egg pods in the field.

Although the effects of resource availability and population density on reproductive allocation have been examined in the mixed-feeder *M. sanguinipes* (Branson, 2003a, b, 2004), which lays fewer and larger egg-pods than *A. deorum*, similar studies need to be conducted on species with different life history patterns. More knowledge is needed on the impact of host plant availability and quality on grasshopper reproductive ecology to increase our understanding of grasshopper population dynamics, and to aid in the development of grasshopper management tools (Joern, 2000). My objective was to examine the effects of population density and increased grass biomass and quality resulting from fertilization on survival, egg pod production and ovariole resorption in *Ageneotettix deorum* (Scudder) (Acrididae).

### Material and Methods

The experiment was conducted on the National Bison Range in northwestern Montana, USA (47°21'6"N, 114°10'30"W), at an elevation of 800 m. Vegetative biomass at this Palouse prairie site was dominated by the grass (Poaceae) species *Agropyron spicatum* (Pursh) Scribn. & J.G. Sm., *Pascopyrum smithii* Rydberg (syn. *Agropyron smithii* Rydberg) and *Poa pratensis* L., while common forbs included *Achillea millefolium* L. (Asteraceae), *Aster falcatus* Lindl. (Asteraceae) and *Erigeron* sp. (Asteraceae). The most common grasshoppers at the site were *A. deorum*, *Melanoplus femurrubrum* (DeGeer), and *M. sanguinipes*. The experimental treatments consisted of ambient-level and fertilized vegetation with two *A. deorum* density levels in a 2 × 2 factorial design. Late instar *A. deorum* were caught with insect nets at an adjacent site with similar vegetation and reared in insect rearing cages in an outdoor laboratory. They were provided with *ad libitum* *A. spicatum*, *E. smithii* and *P. pratensis* until adults. Nymphs were separated by sex before rearing to ensure that females could not mate prior to stocking.

Field cages were placed over similar patches of vegetation which included the dominant grasses at the site. The square 0.1 m<sup>2</sup> cages were constructed of aluminum screening fastened to aluminum garden edging which was buried in the ground and closed with binder clips at the top. Similar cages have been used in a variety of studies with

grasshoppers and have relatively small effects on microclimate (Belovsky and Slade, 1993). Fertilized treatment cages received 250 ml of fertilized water with 0.04% N, by volume, diluted from fish emulsion fertilizer (5-1-1) every two days, while ambient-level treatment cages received no water or fertilizer additions. Although the experiment occurred relatively late in the growing season, the addition of fertilized water doubled the long term average precipitation during the period of the study and was designed to increase per capita host plant availability and quality. Treatments were randomly assigned to cages, and fertilization was initiated July 27th, one week prior to stocking. Newly eclosed adults were stocked in cages at an even sex ratio. The lower density treatment (4 adults per cage, 6 replicates per vegetation treatment) was within the natural range of grasshopper densities present at the site after adjusting for bare ground (Belovsky and Slade, 1995), while the higher density treatment (10 adults per cage, 5 replicates per vegetation treatment) was designed to be above the carrying capacity at the site. There were 3 control cages without grasshoppers for each vegetation treatment. Survival was monitored by counting all grasshoppers within the cages every other day during the 47 day experiment. Males were kept at proportional levels throughout the experiment, by adding or removing males to prevent skewed sex ratios. At the end of the experiment in late September, all surviving females were frozen for reproductive analysis. Cages in which no females survived to the end of the experiment were not used in the reproductive analyses.

At the end of the experiment, green grasses and forbs in each cage were clipped and sorted to determine combined food plant availability and quality. The samples were dried, weighed and ground; and, plant nutritional quality was assessed by 48 hr acid-pepsin digestion of grasses (Terry and Tilley, 1964). Acid-pepsin digestion is correlated with *in vivo* digestibility of vegetation by grasshoppers (Belovsky and Slade, 1995) and the percent digestibility serves as a measure of plant nutritional quality (Bailey and Mukerji, 1976). Host plant availability, as assessed by digestible biomass of grass, was calculated by multiplying grass biomass per m<sup>2</sup> and percent digestibility of grass in a cage (Belovsky and Slade, 1995). After vegetation was clipped, egg pods were removed by sifting through the upper 1.3 cm of sod. An incubator malfunction while incubating egg pods prevented the determination of total egg number. Two reproductive characteristics, resorption bodies and functional ovarioles, were counted through ovary analysis using a dissecting microscope (Launois-Luong, 1978; Branson, 2003a, b). When the process of resorption occurs, the resources in an ovariole are reincorporated and used for egg production or other functions. This process results in a brightly colored resorption body in the pedicel of the ovariole (Launois-Luong, 1978). Functional, or developing, ovarioles are an indication of the size of the next egg pod that would have been laid and are correlated with reproductive output (Uvarov, 1966).

Average survival was calculated by summing the survival days for all females in a cage and dividing by the initial density of females in a cage. Although the experiment was terminated before all females died, the average survival data met distributional assumptions of normality. The per capita rate of egg pod production in a cage was calculated by dividing the number of egg pods by the summed days of survival by all females. This approach corrected for differences in initial density and female survival and allowed an examination of individual-level reproductive allocation responses. Unequal sample size ANOVA models were used to examine treatment effects on digestible grass biomass, percentage digestibility of grass, forb biomass, average days survived by females, proportional survival of females alive at the end of the experiment, and female reproductive characteristics (Quinn and Keough, 2002). Per-capita cage averages

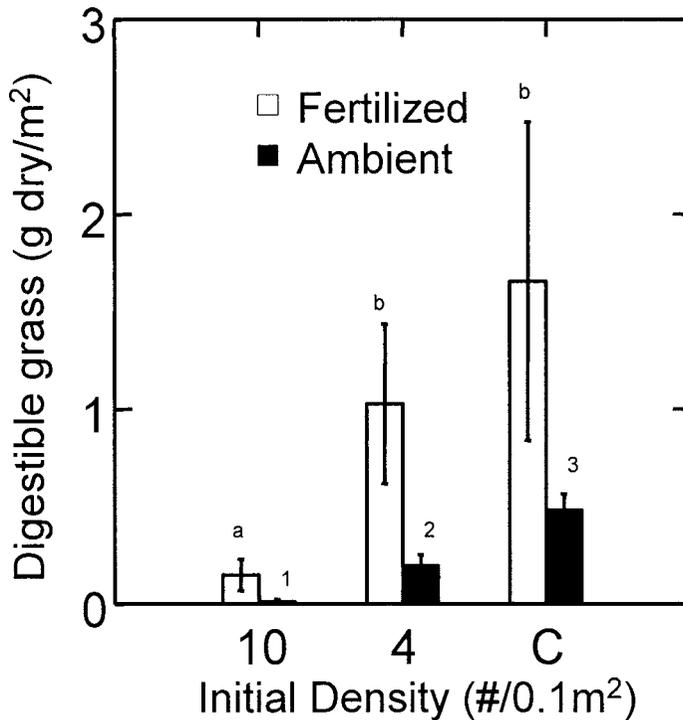


Fig. 1. Total digestible grass biomass (g dry matter/m<sup>2</sup>) for each treatment at the end of the experiment. Vegetation control cages are designated by "C." Values are mean  $\pm$  SE. Treatment means with different letters (fertilized) or numbers (ambient) are significantly different (Sequential Bonferroni,  $P < 0.05$ ).

were used for analyses of egg pod production rate, resorption bodies and functional ovarioles. Proportional data were arcsine square root transformed and digestible grass biomass data were fourth root transformed to meet normality assumptions (Quinn and Keough, 2002). Untransformed data are presented in the figures. The sequential Bonferroni procedure, which adjusts alpha values, was used for multiple pairwise comparisons (Quinn and Keough, 2002). Systat 11 was used for statistical analyses (Systat Software, 2004).

### Results

Digestible grass biomass, a combination of total grass biomass and quality, was used to assess host plant availability. Digestible grass biomass was higher when plants were fertilized (Fig. 1; Table 1). On average, fertilized controls had 340% more digestible grass biomass compared to non-fertilized controls (Fig. 1). As a result, the vegetation treatment was successful in changing host plant availability. The fertilization treatment also increased host plant quality, as the percentage digestibility of grasses averaged 210% higher in fertilized controls than in non-fertilized controls (Table 1). Grasshoppers consumed much of the available grass biomass, with digestible grass biomass 90% lower in the higher density treatment than in controls without grasshoppers (Fig. 1). In addition, digestible grass biomass averaged 85% lower in the higher density level than in the lower density level (Fig. 1; Table 1). Less digestible grass biomass remained in lower density

Table 1. Results of ANOVA models on digestible grass biomass, percentage digestibility of grass, forb biomass, average days of survival, proportional survival, daily per capita rate of egg pod production, per capita resorption bodies and per capita functional ovarioles.

ANOVA tables for:	Source	d.f.	Mean square	F	P
Host Plant Availability (Digestible Grass Biomass)	Resource	1	1.42	16.98	<0.001
	Density	2	1.83	21.97	<0.001
	Interaction	2	0.08	0.21	0.81
% Digestibility of Grass	Resource	1	0.022	11.10	0.003
	Density	2	0.017	8.57	0.002
	Interaction	2	0.002	1.13	0.340
Forb Biomass	Resource	1	38.53	17.54	<0.001
	Density	2	2.86	1.30	0.29
	Interaction	2	1.19	0.54	0.59
Average Female Survival	Resource	1	6.92	0.23	0.64
	Density	1	362.30	11.84	<0.01
	Interaction	1	15.89	0.51	0.48
Proportional Female Survival	Resource	1	5.53	6.19	0.02
	Density	1	7.86	8.69	<0.01
	Interaction	1	0.46	0.51	0.48
Daily Egg Pod Production Rate	Resource	1	$4.1 \times 10^{-3}$	20.84	<0.001
	Density	1	$3.6 \times 10^{-5}$	0.18	0.68
	Interaction	1	$7.6 \times 10^{-5}$	0.38	0.55
Resorption Bodies	Resource	1	194.41	43.78	<0.001
	Density	1	23.70	5.34	0.04
	Interaction	1	5.40	1.21	0.29
Functional Ovarioles	Resource	1	23.88	47.87	<0.001
	Density	1	7.15	14.33	0.002
	Interaction	1	0.003	0.006	0.94

cages than in controls for the ambient-level, but not for the fertilized-level (Fig. 1; Table 1). Forb biomass responded positively to fertilization, but did not respond to the presence of *A. deorum* (Table 1).

Both average female survival and proportional female survival were significantly lower in the higher density treatment (Fig. 2; Table 1), indicative of density-dependent survival. Although average female survival did not significantly respond to increased host plant availability in the fertilized-level treatment (Fig. 2a; Table 1), proportional female survival at the end of the experiment positively responded to food plant availability (Fig. 2b; Table 1). The total number of egg pods recovered per cage was higher in both fertilized-level and higher density treatments (Fig. 3a; Table 1). Daily egg pod production rate positively and significantly responded to host plant availability (Table 1), averaging 64% higher in the fertilized-level treatment than in the ambient-level (Fig. 3b). Daily egg pod production rate did not respond significantly to initial density (Table 1), indicating a lack of density-dependence. The number of resorption bodies significantly responded to both resource and density treatments (Fig. 3c; Table 1). Approximately 54% fewer resorption bodies were detected per-capita in the fertilized-level treatment, while 22% fewer were detected with in the lower initial density treatment (Fig. 3c). Functional ovariole number also responded strongly to increased host plant availability (Table 1) and was approximately 106% higher in the fertilized-level treatment (Fig. 3d). Functional ovariole number negatively responded to initial density (Table 1) and was 45% higher in the lower density treatment

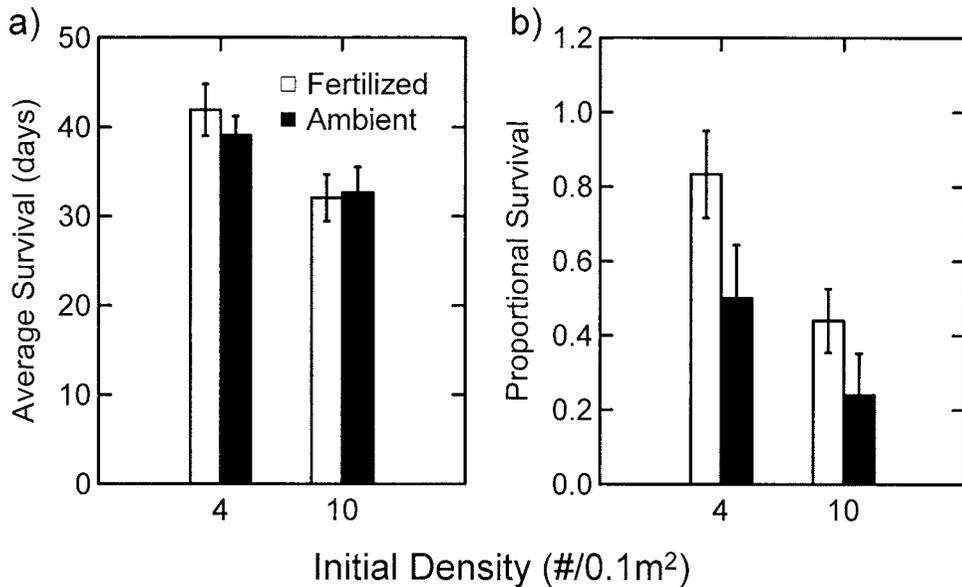


Fig. 2. Average days of female survival and proportional survival at the end of the experiment for each treatment. Values are mean  $\pm$  SE.

(Fig. 3d). Food availability and grasshopper density affected reproductive characteristics in an additive manner, as resource and density treatments did not interact in their effects on reproductive characteristics when both were significant.

#### Discussion

Density-dependent survival was detected, as evidenced by the observed reduction in proportional survival in the higher density treatment. Since much less digestible grass remained in higher density cages (Fig. 1), increased density-dependence prevented females from acquiring enough high quality food (Oedekoven and Joern, 2000). More females remained alive in the higher density than in the lower density treatment at the end of the experiment, indicating that the lower density level was initiated below the carrying capacity at the site (Joern and Klucas, 1993). Proportional survival was lower in the ambient-level treatment (Fig. 2b). As a result, mortality from food limitation occurred near the end of the experiment in the ambient-level treatment. Lower ambient host plant availability than occurred in this study would likely lead to larger differences in average survival between ambient and fertilized treatments, as found by Oedekoven and Joern (2000). The weaker effect of host plant availability on survival, as also found with *M. sanguinipes* (Branson, 2003b), fits predictions from reproductive allocation models that organisms should increase proportional allocation to survival when resources are limited but future reproduction is feasible (Branson, 2001).

All measures of reproduction responded strongly to increased host plant availability in the fertilized-level treatment (Fig. 3). The increased plant biomass with fertilization also included a simultaneous increase in plant quality through the addition of nitrogen fertilizer (Table 1). In contrast to the effects of initial density, the rate of egg pod production averaged 64% higher in the fertilized-level treatment where digestible grass biomass was more abundant (Fig. 3b). Ovarioles that initiated vitellogenesis, but then resorbed or

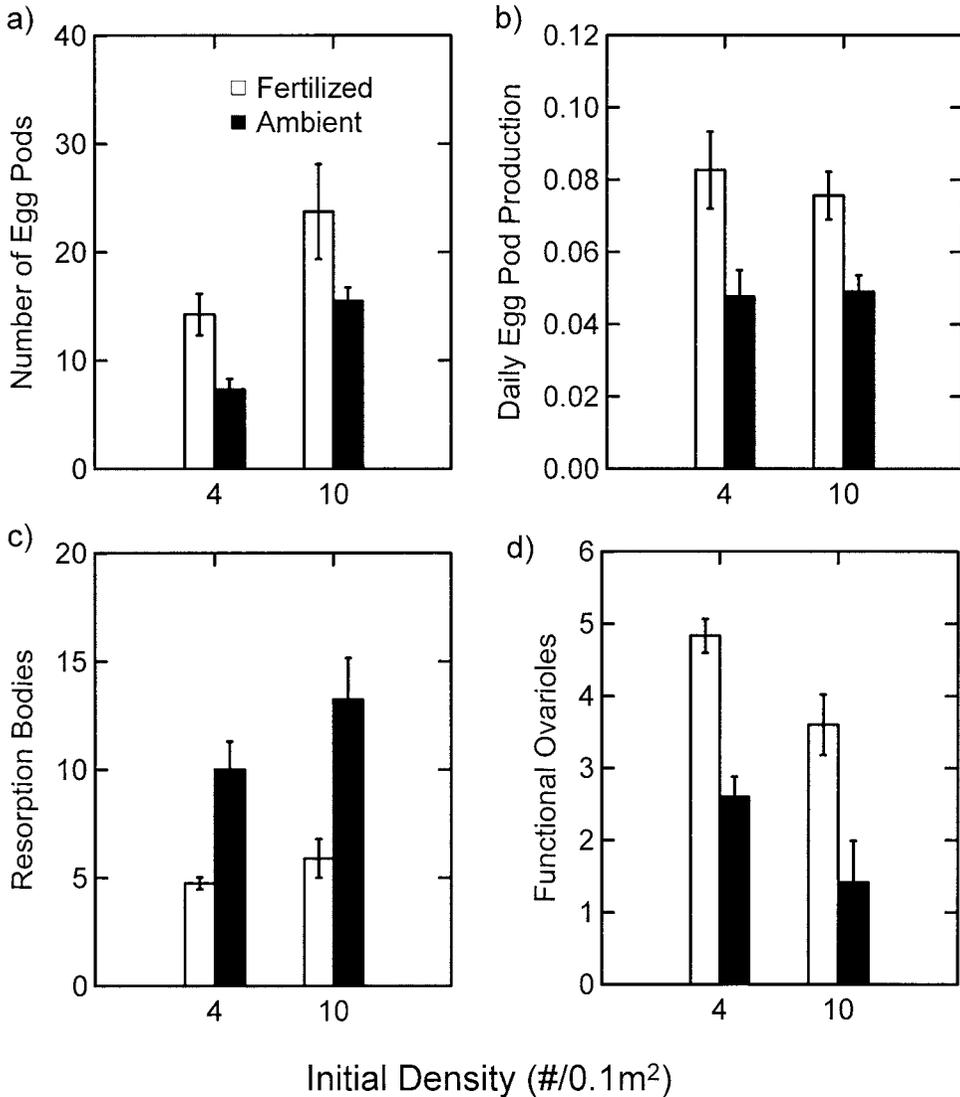


Fig. 3. Total egg pods per cage, daily rate of egg pod production, per capita number of resorption bodies present and per capita number of functional ovarioles present, for each treatment. Values are mean  $\pm$  SE.

reallocated the nutrients, were less abundant with fertilization (Fig. 3c). In addition, the next egg pod to be laid by females in the fertilized-level would have contained nearly twice as many eggs as egg pods in the ambient-level treatment (Fig. 3d). As a result, larger egg pods were laid in the fertilized-level treatment throughout the experiment. An increase of two eggs per pod would have a substantial effect on total reproduction, given that *A. deorum* laid up to 10 egg pods and ovariole number is limited to a maximum of 5 to 6. The increased rate of egg pod production and number of eggs per pod with fertilization demonstrates that reproduction was limited by resource availability in the ambient-level, even though average survival did not respond to food plant availability (Table 1). Percentage digestibility of grasses, although not a direct measure of nitrogen content,

averaged 33% higher in fertilized vegetative controls (Table 1). The strong reproductive response to fertilization indicates that the availability of higher protein resources was the primary limiting factor for egg production of *A. deorum*. These findings agree with those of Joern and Behmer (1997), who demonstrated that the number of eggs per pod and the rate of egg pod production increased with food plant nitrogen content up to ~4–5%. Although Danner and Joern (2004) found no effect of fertilization on egg production of *A. deorum*, their study was conducted during a very dry year when plants were water limited and unable to use the extra nutrients (Danner and Joern, 2004). By initiating the experiment with newly eclosed adults that were all reared on ambient host plants, this experiment isolated the effects of adult resource availability from other factors potentially affecting reproduction. Although Branson (2004) found no carry-over effects of nymphal resource availability on per-capita reproductive allocation of surviving newly eclosed *M. sanguinipes*, Danner and Joern (2004) found reduced nymphal resource availability delayed development and indirectly reduced total egg production of *A. deorum*.

The nature of reproductive allocation responses to resource availability appears to differ slightly between grasshopper species with different life history patterns. In separate studies with the grasshopper *M. sanguinipes* where food plants were watered and fertilized, the rate of egg pod production did not respond to food plant availability or quality as found with *A. deorum* (Branson, 2003b; Branson, 2004). Since *M. sanguinipes* typically produces one to three egg pods under field conditions (Branson, 2003a, b), variability in the rate of egg pod production is likely to be lower than in *A. deorum*. In all cases, grasshoppers responded to increased resource availability by increasing total reproduction.

Density-dependence was not evident in the rate of egg pod production (Fig. 3b; Table 1). However, resorption bodies were approximately 28% higher and functional ovarioles approximately 31% lower at the higher density level (Fig. 3c, d). As a result, egg pods in the higher density level contained fewer eggs per pod throughout the experiment. Although the density-dependent effects on the number of eggs per pod could result from density-dependent behavioral and physiological responses other than exploitative competition (Wall and Begon, 1987; Applebaum and Heifetz, 1999), Branson (2003b) demonstrated that exploitative competition for resources played the primary role in determining reproductive allocation in the grasshopper *M. sanguinipes*. In addition, per capita resource availability explained over 60% of the variation in egg production, with no evidence for interference competition (Branson, 2003b). Very little digestible grass biomass remained in higher density level cages at the end of the experiment (Fig. 1), indicating that food limitation was severe and females were limited in their ability to acquire enough high quality food. For all measures of grasshopper reproductive performance measured, fertilization and density acted in an additive fashion when both were significant. As a result, the primary effects of the higher density level on reproductive allocation likely operated through reduced per capita resource availability leading to increased exploitative competition (Belovsky and Slade, 1995; Branson, 2003b).

Both host plant availability and population density played important roles in the life history variation of *A. deorum*. Given the additive nature of treatment responses, the effects of fertilization and population density treatments on reproductive allocation likely resulted from variation in per capita nutrient availability between treatments, as also found with *M. sanguinipes* (Branson, 2003b). Furthermore, the larger detrimental effects of resource limitation on reproduction than survival suggests that *A. deorum* females could be trading off allocation to reproduction for maintenance in order to increase survival when resources are limited (de Souza Santos and Begon, 1987; Branson, 2003b). From

a population dynamics perspective, the combined patterns of survivorship and fecundity determine the potential number of hatchlings in the next generation. The responses to host plant availability are in accord with Branson (2003b) in suggesting that a large portion of the change in future population densities when resources are limiting may be driven by reduced reproduction, rather than direct mortality. When host plant quality or availability is limited, recruitment can be much lower than would be indicated from assessing peak grasshopper densities. The results are a further demonstration that the reliance on adult densities to predict outbreak risk for the following year, as currently done by USDA-APHIS in the Western U.S., is ineffective. Given the frequent focus on grasshopper survival in field experiments and the highly variable nature of host plant availability, the results will aid in the prediction of climate variation effects on grasshopper population dynamics (Joern, 2000).

#### Acknowledgments

I thank G. Belovsky, J. Chase and J. Slade for assistance in the field. I also thank Andy Lenssen, Greg Sword and two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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