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Source: Journal of Orthoptera Research, 13(2) : 239-245

Published By: Orthopterists' Society

URL: [https://doi.org/10.1665/1082-6467\(2004\)013\[0239:RIONAA\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2004)013[0239:RIONAA]2.0.CO;2)

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Relative importance of nymphal and adult resource availability for reproductive allocation in *Melanoplus sanguinipes* (Orthoptera: Acrididae)

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Abstract

A better understanding of the relative effects that nymphal and adult resource availabilities have on reproductive allocation is needed, given the potentially important implications for the prediction of grasshopper population dynamics. I conducted a field experiment to examine the importance of nymphal and adult resource availabilities on reproductive allocation in the grasshopper *Melanoplus sanguinipes* (Fabricius). Female nymphs were reared on either high or low nymphal resource availability, with watered and ambient-level adult resource treatments. Adult resource treatments were initiated below the carrying capacity, to allow an examination of food limitation effects on reproductive allocation, while minimizing strong density dependent effects. Although nymphs reared with *ad libitum* resources had higher adult body mass, nymphal resource availability did not affect reproductive allocation or adult survival. Female *M. sanguinipes* grasshoppers responded to the increased host plant availability in the watered treatment, by increasing reproduction allocation over the course of the experiment. *M. sanguinipes* females did not reduce vitellogenesis in response to decreased adult resource availability, but completed development of a lower percentage of ovarioles that initiated development. Although resource dynamics in semi-arid grasslands can change rapidly during grasshopper development, there were no direct effects of limited resource availability for developing nymphs that subsequently affected *per capita* reproduction of adults.

Keywords

Melanoplus sanguinipes, reproduction, grasshopper, life history variation, resource availability

Introduction

Grasshoppers exhibit life history variation in response to a variety of resource availability and quality components (Hewitt 1985; Belovsky & Slade 1995; Joern & Behmer 1997, 1998; Stauffer & Whitman 1997; Branson 2003b) and appear capable of adaptive modifications in resource allocation (de Souza Santos & Begon 1987, Branson 2003a). When resources are limiting to an organism, allocation of resources to reproduction unavoidably leads to a reduction in resource allocation to other activities such as survival or maintenance (Nylin & Gotthard 1998). However, the effect of resource availability on reproductive allocation and survival of grasshoppers, often under resource-limited field conditions, has received little attention (Belovsky & Slade 1995, Branson 2003b). Food limitation for high quality resources often exists when initial population densities are below the carrying capacity (Branson 2003b), as grasshoppers selectively forage on plants to maximize survival and reproduction (Bernays & Chapman 1994).

Nymphal resource availability has frequently been assumed to have limited effects on reproductive allocation and adult mortality, because grasshoppers acquire and allocate resources to reproduction primarily as adults (Moehrlin & Juliano 1998). Correlations between phenotypic characteristics thought to be representative of nymphal or adult conditions (such as femur length and body mass) and life history variation have been inconsistent (MacFarlane & Thorsteinson 1980, Atkinson & Begon 1987, Wall & Begon 1987, Sanchez *et al.* 1988). Despite the potential importance for understanding grasshopper population dynamics, the effects of nymphal resource availability on reproductive allocation have not been quantified. Branson (2003b) examined reproductive allocation responses to resource availability and population density in the grasshopper *Melanoplus sanguinipes* (Fabricius) in a field experiment initiated with nymphal grasshoppers, but did not separately examine the effects of nymphal and adult resource availabilities.

Grasshoppers can reduce allocation to reproduction when resources are limiting by decreasing vitellogenesis or increasing oosorption, allowing a higher percentage of resources to be used for other functions such as survival (Chapman 1998, Papaj 2000). Grasshopper ovaries consist of a series of follicles that are capable of developing and producing eggs. Typically not all ovarioles are functional, or developing, at a given time (Bellinger *et al.* 1987). Vitellogenesis occurs when yolk is deposited into an ovarian follicle, initiating development of the follicle (Chapman 1998). In contrast, oosorption, or resorption, occurs when a developing ovarian follicle stops development and the resources in an ovariole are reincorporated and used for egg production or other functions (Joern & Klucas 1993, Chapman 1998, Danner & Joern 2004).

In this study, I examined the relative importance of nymphal and adult resource availabilities for *M. sanguinipes* adult survival and reproductive allocation. I reared nymphal female grasshoppers on 2 resource availability levels in an outdoor laboratory and then conducted a 2 × 2 factorial field experiment, with females from the 2 nymphal rearing treatments placed in watered and ambient-level adult resource treatment cages. The first objective was to examine if reduced resource availability for nymphal females affected *per capita* reproductive allocation or survival of adults. The second objective was to examine how patterns of reproductive allocation changed in response to increased adult host plant availability. The adult resource treatments were initiated below the average carrying capacity at the site to allow an examination of food limitation effects on reproductive allocation, while avoiding strong exploitative competition that can result in high levels of mortality (Joern & Klucas 1993, Belovsky & Slade 1995) and undeveloped ovaries (D. Branson

unpub. data). No field experiments have examined the separate effects of nymphal and adult resource availability on patterns of reproductive allocation, and few experiments have examined if *M. sanguinipes* females respond to variation in host plant availability by changing patterns of oosorption and vitellogenesis (Branson 2003b). A better understanding of the relative effects that nymphal and adult resource availabilities have on reproductive allocation is needed, given the potentially important implications for the prediction of grasshopper population dynamics (Joern 2000).

Materials and Methods

I conducted the experiment at the National Bison Range in north-western Montana, USA, at an elevation of 800 m. The study site consisted of Palouse prairie with plant biomass highly dominated by grasses (Belovsky & Slade 1995). The dominant grass species were *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., *Aster falcatus* Lindl. and *Erigeron* sp. The most common grasshoppers at the site were *M. sanguinipes*, *M. femurrubrum* (DeGeer) and *Ageneotettix deorum* (Scudder). *M. sanguinipes* was used in the experiment and is one of the most common species of rangeland grasshopper in western North America (Pfadt 2002). *Melanoplus sanguinipes* is polyphagous, reproductively plastic (Branson 2003a, b), and lays egg pods ranging from 1 to 36 eggs in the area of the study site (D. Branson unpub. data). In Montana, *M. sanguinipes* has a univoltine life cycle.

The experiment consisted of a 2 × 2 factorial design with 2 nymphal and adult resource treatments. The 2 nymphal rearing resource availability treatments are designated for simplicity as "high" and "low", while the 2 adult host plant availability treatments are designated as ambient-level and watered. I collected early instar *M. sanguinipes* at the experimental site, separated them by sex, and reared them in outdoor insect cages until adult. Low nymphal resource availability female nymphs received approximately 0.5g wet mass of romaine lettuce per individual every 2 d, which was designed to create food limitation for developing nymphs. High resource female nymphs received *ad libitum* romaine lettuce daily. To minimize the potential influence of male condition on female reproduction (Belovsky et al. 1996), all male nymphs were reared on *ad libitum* romaine lettuce. All uneaten food was removed daily from the cages. Romaine lettuce was used as the nymphal rearing food to eliminate nematode parasitism previously encountered when rearing grasshoppers with field vegetation (Belovsky et al. 1997).

I placed 0.1m² basal area cages, with a height of 0.9m, over similar patches of natural vegetation. The cages were constructed of aluminum screening fastened at the base to aluminum garden edging buried in the ground (Belovsky & Slade 1995, Joern & Klucas 1993). Cage effects on microclimate are minimal (Belovsky & Slade 1993). Adult resource availability was supplemented by adding 250 ml of water every other day to the watered treatment cages, which was double the long term average precipitation during the period of the study. The watered resource treatment was designed to examine the effects of increased *per capita* adult resource availability on life history variation with minimal changes in resource quality. Ambient-level treatment cages received no additions. I randomly assigned treatments to cages and initiated the adult resource treatment one week prior to stocking. There were 10 replicates of each treatment combination and 5 vegetation control cages without grasshoppers for both adult resource treatments.

Prior to initiating the field experiment, I randomly chose females

from each nymphal rearing resource treatment and measured the phenotypic characteristics of femur length and body mass. Femur length has been hypothesized to reflect nymphal environmental conditions, with body mass representative of adult condition (Wall & Begon 1987). Two male and 2 female *M. sanguinipes* grasshoppers were added to each cage, which was below the average long-term carrying capacity at the site when adjusted for vegetative cover (Belovsky & Slade 1995). The initial density was chosen to minimize strong density-dependent effects on survival and reproduction, while allowing an examination of reproductive allocation responses to resource limitation. I counted the adult resource treatment cages and accounted for all individuals in each cage daily to determine grasshopper survival (Belovsky & Slade 1995). I maintained an even sex ratio throughout the experiment by adding or removing males, as mating frequency has been shown to affect reproductive effort and female survival (Pickford & Gillot 1972).

Diet-induced phenotypic plasticity in mandible structure has been demonstrated with *Melanoplus femurrubrum* (Thompson 1999). To examine if rearing nymphs on romaine lettuce affected the survival and reproduction of female *M. sanguinipes* foraging on field vegetation in cages, I caught newly eclosed females which had not mated and stocked them in field cages, following the protocol described above. Survival and reproduction of adults did not vary between females reared on romaine lettuce and field-caught newly eclosed females (ANOVA, $p > 0.6$).

I clipped green vegetation in each treatment and control cage at the end of the experiment and separated it by grasses and forbs. I dried, weighed, and ground vegetation samples. I then assessed nutritional quality of grasses by acid-pepsin digestion (Terry & Tilley 1964, Bailey & Mukerji 1976). Acid-pepsin digestion is correlated with *in vivo* digestibility of vegetation by grasshoppers and serves as a measure of plant nutritional quality for grasshoppers (Belovsky & Slade 1995). I did not examine forb nutritional quality due to the limited number of cages where sufficient forb biomass remained at the end of the experiment.

At the end of the experiment (late September), I removed and froze all surviving adults. I measured reproductive characteristics through ovary analysis using a dissecting microscope (Launois-Luong 1978; Joern & Klucas 1993; Branson 2003a, b). When an egg is released into the oviduct, the covering of the egg compresses into a visible band called the follicular relict. A brightly colored resorption body is apparent when an ovarian follicle stops development and nutrients are reallocated from the follicle. For each female, I determined total *per capita* egg production by counting the number of follicular relicts present in the ovarioles of a given female. The total number of ovarioles initiating vitellogenesis was calculated by combining the numbers of follicular relicts and resorbed ovarian follicles. I also counted the number of functional or developing ovarioles, which is an indication of the size of the next egg pod to be laid had the experiment not been terminated.

I used unequal sample size ANOVA models to examine nymphal and adult resource treatment effects on vegetation characteristics. Due to low forb biomass in cages, I used Chi-Square analysis to examine if the presence or absence of forbs differed between ambient-level and watered resource level treatments. I used logistic regression analysis to examine if the nymphal and adult resource treatments affected whether 0, 1, or 2 females survived to the end of the experiment. I used multivariate analysis of variance (MANOVA) to assess overall treatment effects on both reproductive allocation characteristics and prestocking measurements, because multiple characteristics were measured on individual grasshoppers (Zar

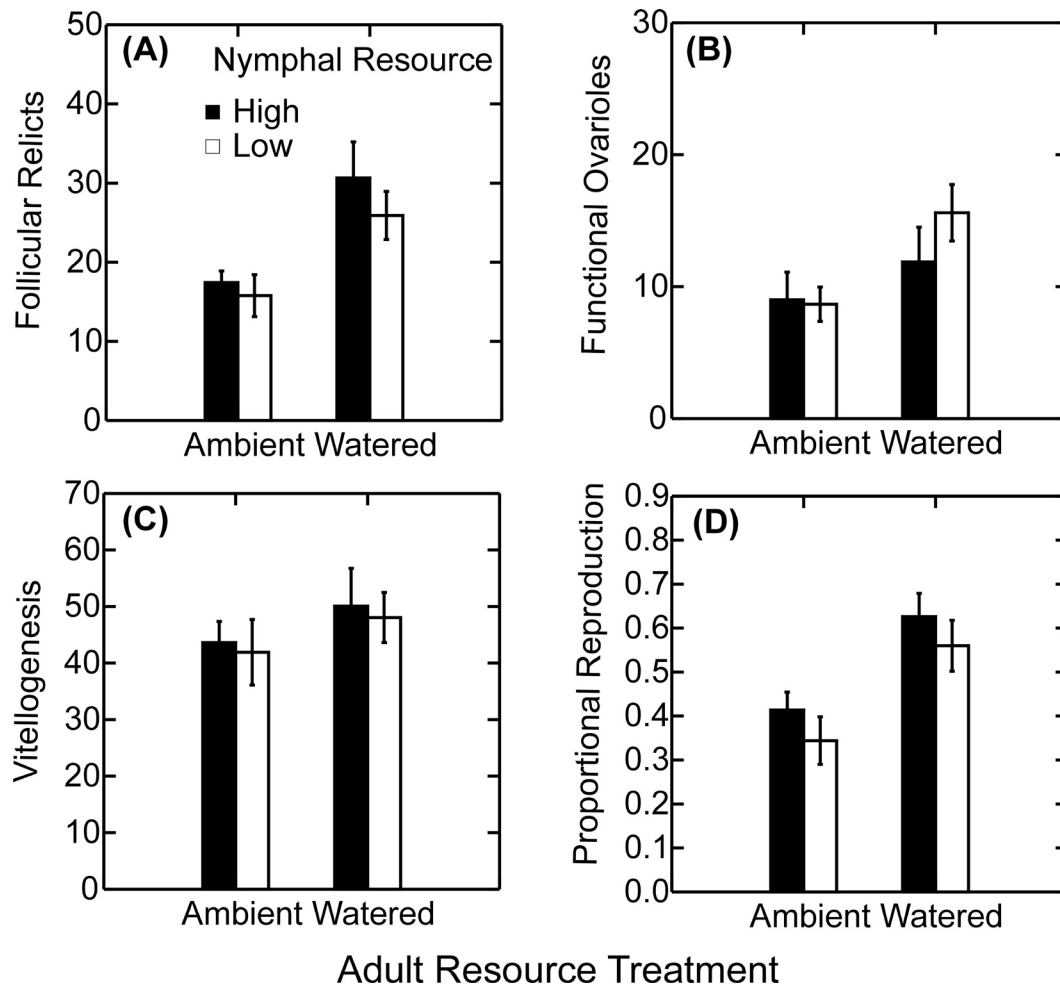


Fig. 1. Reproductive allocation in response to nymphal and adult resource availability treatments for females surviving to the end of the experiment. All results are based on *per capita* cage averages. Values are means ± 1 s.e. A. Average number of follicular relicts (eggs laid). B. Average number of functional ovarioles. C. Average number of follicles initiating vitellogenesis. D. Average proportion of initiated follicles completing development (follicular relicts/vitellogenesis).

1999). If a MANOVA model was significant, univariate analyses of variance were used to assess treatment differences on individual reproductive characteristics or prestocking measurements (Zar 1999). Cages where no females survived to the end of the experiment were not utilized for reproductive analyses. Vegetation data were log-transformed as necessary to normalize values. I used cage means as replicate values for all analyses, as the experiment was designed to examine *per capita* reproductive responses. I used SYSTAT 10 (SPSS Inc. 2000) for all statistical analyses.

Results

Nymphal resource availability significantly affected phenotypic characteristics of females prior to stocking, based on a multivariate analysis (Table 1). Females reared with higher resource availability had a greater body mass than females reared with lower resource availability (Table 1). There was a marginal positive effect of increased nymphal resource availability on adult femur length (Table 1).

Both grass biomass and the percentage digestibility of grass were lower when grasshoppers were present than in vegetation control cages (Table 2). When grasshoppers were present, watered treat-

ment cages had higher biomass, but similar plant quality, as ambient-level treatment cages (Table 2). Averaged across all treatments, total green biomass at the end of the experiment was composed of over 90% grass biomass. When treatment cages with grasshoppers were analyzed for the presence or absence of forbs, fewer cages in the ambient-level resource treatment had forbs present than in the watered resource treatment ($X^2 = 21.665$, $p < 0.001$). All watered treatment cages with grasshoppers had forbs present, and all control cages in both treatments had forbs present.

Nymphal resource availability treatments did not significantly affect whether 0, 1 or 2 females survived to the end of the experiment (Logistic Regression: Wald Chi-Square = 1.755, $p = 0.185$). In addition, female survival was not significantly affected by the adult resource treatments (Logistic Regression: Wald Chi-Square = 0.479, $p = 0.488$). Based on a multivariate analysis, reproductive characteristics of *M. sanguinipes* females were not significantly affected by nymphal resource treatments (Table 3). However, adult resource availability significantly affected reproductive characteristics of *M. sanguinipes* (Table 3). Females in the watered treatment laid approximately 68% more eggs than females in the ambient-level treatment, as measured by numbers of follicular relicts (Fig. 1A, Table 3). Functional ovariole number was higher in watered adult

Table 1. A) Statistical results of female phenotypic characteristics. B) Mean and standard deviation values for femur length (mm) and body mass (g) from prestocking phenotypic measurements of female grasshoppers in high and low nymphal rearing treatments.

A.	MANOVA	Factor	df	Wilks' Lambda	F	p
	Phenotypic Measurements	Nymphal Resources	3,32	0.463	12.396	<0.001
	Univariate F Tests for:	Factor	df	Mean Square	F	p
	Femur Length	Nymphal Resources	1	0.001	3.366	0.075
	Body Mass	Nymphal Resources	1	0.046	34.052	0.001
B.		High Nymphal		Low Nymphal		
	Femur Length (mm)	12.82 ± 0.56		12.52 ± 0.48		
	Body Mass (g)	0.344 ± 0.043		0.272 ± 0.032		

Table 2. A) ANOVA results for green grass biomass and percent digestibility of grass remaining in cages at the end of the experiment. B) Mean values for total grass biomass (g dry/m²) and percent digestibility of grass at the end of the experiment for each adult resource and grasshopper herbivory treatment combination.

A.	Analysis of:	Factor	df	Mean Square	F Value	p value
	Grass Biomass	Herbivory	1	52.645	40.518	<0.001
		Adult Resource	1	6.056	4.664	0.03
		Interaction	1	0.002	0.002	0.97
	% Digestibility	Herbivory	1	1.6x10E-3	14.58	<0.001
		Adult Resource	1	8.0x10E-4	0.733	0.40
		Interaction	1	9.3x10E-5	0.085	0.77
B.	Resource	Herbivory	Grass Biomass	% Digestibility		
	Natural	Control	4.36 ± 1.22	0.303 ± 0.022		
	Natural	Grasshopper	2.50 ± 0.98	0.257 ± 0.037		
	Watered	Control	5.01 ± 1.78	0.310 ± 0.023		
	Watered	Grasshopper	3.12 ± 0.99	0.270 ± 0.030		

Table 3. Statistical results of *per capita* reproduction-related parameters for females removed at the end of the experiment. All results are based on *per capita* cage averages.

MANOVA	Source	df	Wilks' Lambda	F	p
Reproductive Characteristics	Adult Resource	3,28	0.600	6.211	0.002
	Nymphal Resource	3,28	0.870	1.399	0.264
	Interaction	3,28	0.921	0.797	0.506
Univariate F Tests for:	Factor	df	Mean Square	F	p
Follicular Relicts	Adult Resource	1	1136.142	16.848	0.001
Functional Ovarioles	Adult Resource	1	166.617	5.111	0.03
Vitellogenesis	Adult Resource	1	131.653	0.864	0.36

resource females (Fig. 1B, Table 3), indicating that the next egg pod to be produced in the watered treatment, had the experiment not been terminated, would have been approximately 58% larger. Since vitellogenesis was not affected by adult resource availability (Fig. 1C, Table 3), while egg production was (Fig. 1A), females in the watered treatment completed development of a higher percentage of ovarioles initiating vitellogenesis (follicular relicts/vitellogenesis) (Fig. 1D). Therefore, grasshoppers did not significantly increase their rate of vitellogenesis in response to increased host plant availability, but more frequently completed development of eggs. Nymphal and adult resource availabilities did not significantly interact in their effects on either reproductive allocation (Table 3) or female survival (Logistic Regression: Wald Chi-Square = 0.0159, $p = 0.900$). As a result, females reared with low nymphal resource availability did not exhibit additional reductions in survival or reproduction when stocked as adults in ambient-level treatment cages.

Discussion

Impact of Nymphal Resource Availability.—Although nymphal resource availability was positively related to grasshopper mass, with a marginal effect on femur length (Table 1), this did not translate into differences in adult survival or reproduction (Table 3). Femur length has been hypothesized to reflect nymphal environmental conditions (Wall & Begon 1987), and femur length was shorter in the low nymphal resource treatment. However, there was no indication that the smaller structural size of females reared with lower resource availability was associated with reduced reproductive allocation. *M. sanguinipes* females reared with low nymphal resource availability did not have a higher percentage of undeveloped ovarioles (Fig. 1B), and there were no indications of an increased preoviposition period. As reduced resource availability during nymphal rearing did not affect the reproductive allocation of females surviving until adults, it appears resource allocation to reproduction was not significant until *M. sanguinipes* were adults. Although *M. sanguinipes* females appeared to both acquire and allocate resources to reproduction once adults (Moehrlin and Juliano 1998, Hatle *et al.* 2004), females reared with low nymphal resources could have also compensated for nutritional deficiencies by modifying patterns of food intake, either during nymphal rearing or after females were placed in field cages. Grasshoppers and locusts can compensate for diet deficiencies by increasing consumption, modifying food selection, and modifying postingestive processes (Reviewed in Bernays & Simpson 1990, Simpson *et al.* 1995). In addition, inherited environmental effects resulting from nymphal resource availability, could affect life history characteristics of *M. sanguinipes* offspring in the following year, but were not examined (Smith 1972, Rossiter 1996).

Adult Resource Availability.—Less grass biomass remained in cages with grasshoppers present than in vegetation control cages (Table 2), indicating that grasshopper herbivory reduced vegetative biomass throughout the experiment. The percentage digestibility of grass was lower in cages with grasshoppers present than in vegetation control cages (Table 2), which is consistent with grasshoppers selectively removing the highest quality portions of plants (Chapman 1990). *M. sanguinipes* is a polyphagous species, feeding on a number of grasses and forbs (Pfadt 2002). Since forbs were present in all cages in all control cages and in all watered treatment cages with grasshoppers, but in less than 30% of the cages with grasshoppers in the ambient-level treatment, *M. sanguinipes* appeared to have actively foraged on limited forb biomass. The combined biomass,

abundance and quality results are consistent with grasshoppers being food-limited during the experiment, even though the experiment was initiated below the carrying capacity. Branson (2003b), in an experiment with *M. sanguinipes* at a nearby site, demonstrated that exploitative competition for high quality resources occurred even when grass biomass was abundant.

Grass biomass at the end of the experiment was more abundant in watered treatment cages, but the percent digestibility of grass did not differ significantly between resource treatments (Table 2). Forbs can be a high nutritional content food source, and forb availability was also higher in the watered treatment. These results demonstrate that the watering treatment increased host-plant availability during the experiment, while not significantly affecting grass quality. The addition of water in prairie systems frequently results in increased grass biomass and reduced nitrogen content (Mattson & Haack 1987, Belovsky & Slade 1995, Joern & Mole forthcoming), presumably due to nitrogen limitation. However, environmental conditions appear to interact with water additions in their effects on nitrogen content, which can lead to variable results between years (Belovsky & Slade 1995, Joern & Mole in press). Levels of water addition higher than those used in this experiment would likely result in reduced nitrogen content of grasses. In summary, the decreased presence of forbs in ambient-level treatment cages and increased grass biomass in watered control cages indicate that the watered treatment increased host-plant availability of both grasses and forbs.

Impact of Adult Resource Availability.—Although there was no relationship between nymphal or adult resource treatments and whether 0, 1 or 2 females survived in a cage, the detection of statistically significant differences would be unlikely given the initial density of 2 females per cage. The adult resource treatments were initiated below the long-term carrying capacity, to allow an examination of food limitation effects on reproductive allocation, while avoiding strong exploitative competition and density-dependent mortality. As a result, conclusions regarding the effects of resource availability on patterns of mortality are unwarranted.

Female *M. sanguinipes* grasshoppers responded to the increased host plant availability in the watered treatment by increasing reproduction allocation over the course of the experiment. Nymphal and adult resource availabilities did not interact in their effects on reproductive allocation (Table 3). Egg production in *M. sanguinipes* was higher in the watered treatment (Table 3, Fig. 1A), indicating that resource availability in the ambient-level treatment appeared limiting to reproduction. The higher egg production in the watered treatment could have been in response to either the increased grass biomass or availability of forbs. Even when grass biomass appeared abundant, Branson (2003b) found *per capita* resource availability explained over 60% of the variation in egg production in *M. sanguinipes*. Female *M. sanguinipes* in the watered treatment did not increase the initiation rate of follicles (vitellogenesis), but completed development of a higher percentage of ovarioles that initiated development (Table 3, Fig. 1C, D). Even if the amount of energy recovered by resorbing oocytes is small, future resource demands for reproduction would be significantly reduced for females in the ambient-level resource treatment, allowing resources to be allocated to survival (Branson 2001). Because *M. sanguinipes* often only produces 1 to 3 egg pods under field conditions (Branson 2003b), reductions in vitellogenesis in the ambient-level resource treatment would likely occur only under more severe food limitation than occurred in this study. Functional ovariole number, an indica-

tion of future reproduction, was higher in females in the watered resource treatment (Table 3, Fig. 1B), further evidence that females in the ambient-level treatment were food-limited at the end of the experiment. As a result, females with higher host plant availability from watering would continue to lay a higher percentage of the eggs initiated.

Conclusion

Grasshoppers with lower food availability as nymphs had similar reproduction to those who experienced high food availability while nymphs, regardless of adult resource availability. Female *M. sanguinipes* responded to increased adult resource availability by increasing reproductive allocation, even when initiated below the average carrying capacity at the site. Reduced nymphal food availability likely affects grasshopper population dynamics in ways that were not addressed by this study, as reduced *per capita* resource availability leads to increased nymphal mortality rates (Belovsky & Slade (1995) and development times (Danner & Joern 2004). Danner and Joern (2004) found resource limitation for nymphal *A. deorum* grasshoppers led to delayed development and indirectly reduced total reproduction. Resource dynamics in semi-arid grasslands can change rapidly due to precipitation throughout the period when nymphal grasshoppers are developing (Joern 2000). However, these results indicate that there were no direct residual effects of limited resource availability for developing nymphs that subsequently affected *per capita* reproduction of adults.

Acknowledgements

Gary Belovsky, Jon Chase and Jennifer Slade provided assistance in the field. I wish to thank Gary Belovsky, Dave Kazmer, Gene Schupp, Tom Shanower and 2 anonymous reviewers for their comments on this manuscript.

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