Reproduction and survival in *Melanoplus sanguinipes* (Orthoptera: Acrididae) in response to resource availability and population density: the role of exploitative competition

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Abstract—The relative importance of exploitative competition for resources on grasshopper reproductive allocation has not been fully examined. Given the large fluctuations in grasshopper densities that periodically occur in western North America, an increased understanding of how grasshopper survival and reproduction vary in response to intraspecific densities and per capita resource availability is important. I examined if exploitative resource competition could explain variation in reproductive allocation in *Melanoplus sanguinipes* (Fabricius) in response to resource availability and grasshopper population density. I also examined whether individual differences in competitive ability resulted in increased variance in egg production with low per capita resource availability. As expected with exploitative resource competition, per capita resource availability explained a significant amount of the variation in all reproductive characteristics examined. There was no effect of per capita resource availability on survival. Residuals of the regressions of egg production and vitellogenesis *versus* per capita resource availability did not differ for resource or density treatments, indicating that exploitative competition for resources played a more important role than interference competition in determining reproductive allocation in *M. sanguinipes*. Individual differences were evident, as variation around the mean of egg production increased with resource limitation. Exploitative competition for resources was important in determining both individual and population-level reproductive responses of grasshoppers to resource availability.

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Résumé—L'influence relative de la compétition d'exploitation pour les ressources sur le budget de la reproduction n'a jamais été examinée en détail. Étant donné les fluctuations importantes de la densité des criquets migrateurs qui se produisent périodiquement dans l'ouest de l'Amérique du Nord, il est devenu nécessaire de mieux comprendre comment la survie et la reproduction varient en fonction des densités intraspécifiques et de la disponibilité des ressources per capita. J'ai cherché à déterminer si la compétition d'exploitation pour les ressources peut expliquer la variation dans le budget de la reproduction chez *Melanoplus sanguinipes* (Fabricius) en fonction de la disponibilité des ressources et de la densité de la population de criquets. J'ai examiné aussi si les différences individuelles de la capacité de compétition entraînent une augmentation de la variance dans la production d'oeufs lorsque la disponibilité des ressources per capita est faible. Comme on pouvait s'y attendre avec la compétition d'exploitation, la disponibilité des ressources per capita explique une partie importante de la variation de toutes les caractéristiques de la reproduction. La disponibilité des ressources per capita est sans effet sur la survie. Les résidus des

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régressions de la production d'oeufs et de la vitellogenèse en fonction de la disponibilité des ressources per capita ne diffèrent pas aux divers niveaux des ressources ou de la densité, ce qui indique que la compétition d'exploitation joue un plus grand rôle que la compétition d'interférence dans la détermination du budget de la reproduction chez *M. sanguinipes*. Il y a des différences individuelles importantes : en effet, plus les ressources sont limitées, plus la variation autour de la moyenne de la production d'oeufs est grande. La compétition d'exploitation pour les ressources joue un rôle important dans la détermination des stratégies reproductives en fonction de la disponibilité des ressources chez les criquets migrateurs, tant à l'échelle de l'individu qu'à celle de la population.

[Traduit par la Rédaction]

Introduction

Considerable research has been conducted on the population dynamics of grasshoppers, but our ability to predict rangeland grasshopper population dynamics has been hampered by a limited understanding of the underlying mechanisms responsible (Lockwood 1997; Joern 2000). Grasshopper life histories vary in response to a number of factors such as population density, resource availability, and thermal conditions (Belovsky and Slade 1993; Joern and Klucas 1993; Joern and Behmer 1998; Willott and Hassall 1998). Much rangeland vegetation has low nitrogen or reduced quality that can reduce grasshopper reproduction and survival (Smith and Northcott 1951; Joern and Behmer 1998). Differences in per capita resource availability lead to differing life-history patterns in many organisms (Monson *et al.* 2000), but the effects of per capita resource availability on grasshopper reproductive allocation under field conditions have received limited attention. In one of the few field experiments to date, resource addition led to increased grasshopper survival and functional ovariole number (Belovsky and Slade 1995).

Although the effects of intraspecific and interspecific grasshopper densities on survival have frequently been examined in the field (Evans 1992; Ritchie and Tilman 1992; Chase and Belovsky 1994), variation in reproduction in response to intraspecific density has received limited attention (Joern and Klucas 1993). Additionally, most studies examining the effects of intraspecific grasshopper density on life-history variation have failed not only to determine per capita resource availability but also to separate the role of exploitative resource competition from other density-dependent effects (Wall and Begon 1987; Applebaum and Heifetz 1999). Exploitative competition should occur in years or under conditions when the availability of high-quality food is limited (Joern 2000). Per capita resource availability declines with increasing intraspecific grasshopper densities beyond the density where food limitation begins, resulting in reduced survival or reproduction or both when exploitative competition is dominant (Belovsky and Slade 1995). However, food limitation can also arise from digestive processing constraints independent of resource availability (Stephens and Krebs 1986). A number of additional density-dependent behavioral and physiological life-history responses, including interference competition, can affect grasshopper and locust population dynamics (Applebaum and Heifetz 1999).

Mean measures of reproductive allocation can be used to predict population dynamics (Joern and Gaines 1990); however, variation in reproduction allocation among individuals has important implications for our understanding of life-history variation and life-history evolution. Average per capita resource availability declines with increasing population densities, but individuals can differ in their ability to exploit resources. Less competitive individuals acquire fewer resources when resources are limiting (Lomnicki 1980; Belovsky *et al.* 1996). Competitively superior individuals will have higher reproduction or survival (Belovsky *et al.* 1996) than expected from treatment mean values, resulting in increased variance around the mean (Crowl *et al.* 1997; Callaghan and Hollaway 1999).

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). Grasshopper ovaries consist of a series of ovarian follicles that are typically not all functional (Bellinger *et al.* 1987). When an egg is released into the oviduct, the egg covering compresses into a narrow visible band called the follicular relict. 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. After a given developmental stage of vitellogenesis, however, allocation to a follicle may become fixed (Moerhrlin and Juliano 1998).

I examined the effects of per capita resource availability and the importance of exploitative resource competition on *Melanoplus sanguinipes* (Fabricius) survival and reproductive allocation. No field experiments to date have examined how patterns of vitellogenesis, resorption, and oogenesis of *M. sanguinipes* change in response to per capita resource availability. Additionally, an increased understanding of the importance of exploitative competition on life-history variation in *M. sanguinipes* has important implications for predicting grasshopper population dynamics (Joern and Behmer 1998).

Materials and methods

Study site

I conducted the experiment in a Palouse prairie at the National Bison Range in northwestern Montana, United States of America (47°21′6′′N, 114°10′30′′W), at an elevation of 800 m. Vegetative biomass at the site was dominated by the grass species *Poa pratensis*, *Elymus spicatum*, and *Elymus smithii*. During July and August 1993, precipitation was 7.7 cm higher than the long-term mean of 5.8 cm and average maximum daily temperature was 8°C cooler than the long-term average. Grasshopper densities at the site ranged from less than 2 to 70 fourth- and fifth-instars per m^2 (Belovsky and Joern 1995; Belovsky and Slade 1995), and averaged 18 per m^2 when the experiment was initiated. The most common grasshoppers at the site were *M. sanguinipes*, *Melanoplus femurrubrum* (DeGeer), and *Ageneotettix deorum* (Scudder). *Melanoplus sanguinipes* is polyphagous, eating both grasses and forbs, and is the most common species of rangeland grasshopper in much of western North America (Pfadt 1994). It exhibits reproductive plasticity (Dingle *et al.* 1990) and typically lays one to three egg pods with up to 34 eggs under field conditions in western Montana (Branson 2001).

Experimental procedures

I used 0.36-m^2 cages constructed of aluminum screening to study grasshopper responses to intraspecific density and resource availability. I placed each cage over a patch of vegetation that included the dominant grasses and forbs at the site, but I did not assess vegetative biomass or relative species abundances in each cage. Treatments were randomly assigned to cages after they were installed. The square cages were constructed of aluminum screening fastened to aluminum garden edging, which was buried in the ground. Similar cages have been used in a variety of studies with grasshoppers and have little effects on microclimate (Belovsky and Slade 1993). The experiment used a 2 × 2 fully factorial design with five replicates of two resource (natural, increased) and five density treatments (6, 10, 16, 22, 32). I added 1000 mL of water with 0.04% N, by volume, to the increased resource treatment cages every other day starting 1 week prior to stocking. I collected fourth-instar *M. sanguinipes* at the site in early July, held them in terrariums for 24 h to minimize poststocking mortality that was due to field collection, and stocked cages at an even sex ratio. I established vegetation control cages without grasshoppers for each resource treatment and conducted cage counts to assess grasshopper survival. Although a number of cages were damaged during the experiment and were excluded from analyses, three cages remained in all but one treatment combination.

I removed all surviving adults in late September and measured female reproductive characteristics through ovary analysis (Launois-Luong 1978; Bellinger and Pienkowski 1985). Grasshopper ovaries are composed of a series of panoistic ovarioles, each opening separately into one of two oviducts (Chapman 1998). I determined total per capita egg production by counting the number of follicular relicts present in the ovarioles of a given female. I determined the per capita total number of ovarioles initiating vitellogenesis during the experiment by combining the numbers of follicular relicts and ovarian follicles that had resorbed. I counted the number of functional or developing ovarioles in each female, which is an indication of the size of the next egg pod that would have been laid. I also calculated the proportion of initiated follicles completing egg development (follicular relicts / vitellogenesis). At the end of the experiment, I clipped and sorted green grasses and forbs in each cage. I weighed, ground, and assessed plant nutritional quality by acid–pepsin digestion of grasses and forbs (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). I calculated total digestible biomass by combining the products of grass biomass and its percent digestibility with forb biomass and its percent digestibility (Belovsky and Slade 1995). I divided the total digestible biomass in a cage by the initial grasshopper density to determine per capita resource availability.

Analysis and predictions

I used unequal sample size ANOVA models to examine treatment effects on egg production and numbers of grasshoppers surviving (SPSS Inc 2000). I used linear regression to assess the relationship between survival measures and either per capita digestible biomass or initial treatment density. I used linear regression to assess the relationship between per capita resource availability measurements and reproductive characteristics (Zar 1999), and analyzed the regression residuals as dependent variables in ANOVA models with resource and density treatments (Draper 1981). I used paired *t* tests to determine if the slopes of the regression lines differed between resource treatments (Zar 1999). If exploitative resource competition was important in determining reproductive allocation, I predicted per capita resource availability should explain a significant amount of the variation in reproductive characteristics and the residuals of the regressions on reproductive characteristics should not differ between density treatments. Significant differences in residuals would indicate that other density-dependent factors such as interference competition had affected reproductive allocation. The increased resource treatment could change a number of plant characteristics affecting *M. sanguinipes* reproduction, such as carbohydrate, mineral, secondary compound, structural, and fatty-acid composition (Chapman 1990; Muralirangan *et al.* 1997; Joern and Behmer 1998). If plant characteristics change as a result of the increased resource treatment in ways that affect *M. sanguinipes* reproduction but are not detected by the acid–pepsin quality assessment, I predicted the residuals from the regressions on reproductive characteristics would differ between resource treatments.

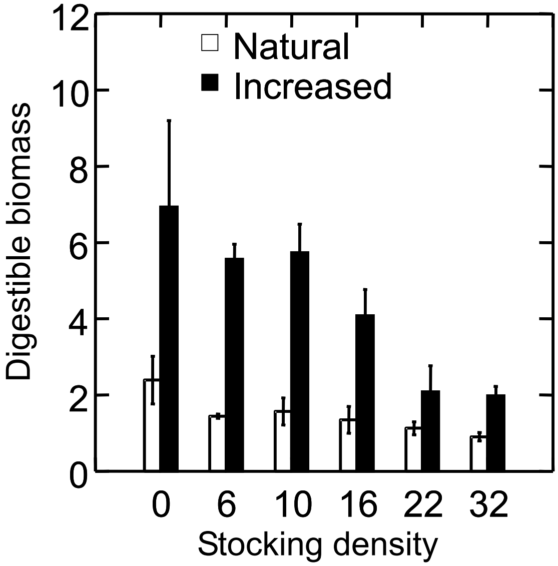

FIGURE 1. Total digestible vegetation biomass (g dry/m^2) for each treatment at the end of the experiment. Vegetation control cages are designated with an initial density of zero. Values are means ± SE.

The coefficient of variation (CV) is a simple and robust estimate of variability that scales the variance by the value of the sample mean (McCardle *et al.* 1990). If individual differences in competitive ability were significant, I predicted that the CV of follicular relicts would be higher when resources were strongly limiting. I used ANOVA tests with the CVs as the dependent variable to examine this prediction and used Tukey's HSD (protected *P* values) to make pairwise *post-hoc* comparisons (Zar 1999). SYSTAT version 10 (SPSS Inc 2000) was used for all statistical analyses.

Results

Resource availability

Digestible vegetation in cages at the end of the experiment differed among both resource and density treatments with a significant interaction resulting from large biomass reductions at high population densities in the increased resource treatment (Fig. 1, Table 1). Digestible plant biomass was abundant in cages stocked at higher densities at the end of the experiment (Fig. 1). Percent digestibility of grass was higher in the increased resource treatment (Table 1). In the increased resource treatment, cages initiated at the highest density (32) had lower digestibility of grass than in the three lowest density treatments (Table 1). Percent digestibility of grass in the highest density treatment in both resource treatments was lower than in control cages with no grasshoppers present (Table 1). Vegetation biomass was at the upper end of the range of vegetation biomass documented at the site (Belovsky and Slade 1995).

Grasshopper survival

There was a significant linear relationship between initial population densities and numbers of *M. sanguinipes* surviving in both resource treatments, with initial densities explaining approximately 80% of the variation in numbers surviving (Fig. 2). Final densities did not crash or converge to similar levels in the highest density treatments

TABLE 1. ANOVA and pairwise comparison results for digestible vegetation, percent digestiblity of grass, grasshopper survival, numbers of follicular relicts, and the coefficient of variation (CV) in follicular relicts.

(*a*) ANOVA results based on per capita mean values per cage.

	Source	df	MS	*F*	*P*
Digestible vegetation	Resource	1	40 519	105.78	<0.001
	Density	5	4 648	12.14	<0.001
	Interaction	5	2 003	5.23	0.001
Percent digestibility	Resource	1	0.044	85.64	<0.001
	Density	5	0.006	8.94	<0.001
	Interaction	5	0.001	0.75	0.590
Average survival	Resource	1	8.09	1.72	0.198
	Density	4	379.2	80.8	<0.001
	Interaction	4	6.16	1.31	0.285
Follicular relicts	Resource	1	660.7	15.18	<0.001
	Density	4	330.3	7.6	0.01
	Interaction	4	28.13	0.66	0.630
CV of follicular relicts	Resource	1	0.845	7.538	0.013
	Density	4	0.513	4.576	0.009
	Interaction	4	0.112	0.999	0.433

(*b*) Pairwise mean differences and comparison of *P* values for grass percent digestibility.*

	Pairwise mean difference (treatment 1 – treatment 2)	*P*
Natural 0 *vs.* 22	+0.047	0.118
Natural 0 *vs.* 32	+0.072	0.005
Increased 0 *vs.* 22	+0.049	0.169
Increased 0 *vs.* 32	+0.083	0.003
Increased 6 *vs.* 32	+0.060	0.025
Increased 10 *vs.* 32	+0.068	0.009
Increased 16 *vs.* 32	+0.062	0.018

(*c*) Pairwise comparison of CV of follicular relicts in natural resource treatments.*

	P
Natural 6 *vs.* 32	0.10
Natural 10 *vs.* 32	0.04

(*d*) CV of follicular relicts in natural resource treatments.

	Mean ± SD
Natural 6	0.617± 0.392
Natural 10	0.341±0.403
Natural 32	1.461±0.312

* Tukey's HSD with protected *P* values, $P \leq 0.2$.

(Fig. 2). The initial differences in populations persisted throughout the experiment, as there was a significant effect of density treatments on number surviving (Table 1). In addition, the slopes of the regression lines did not differ between the two resource treatments ($t = 1.193$, $P > 0.2$, $n = 42$). Numbers of *M. sanguinipes* surviving did not differ between resource treatments and, although there was a trend towards higher survival at high density in the increased resource treatment, the interaction between resource level

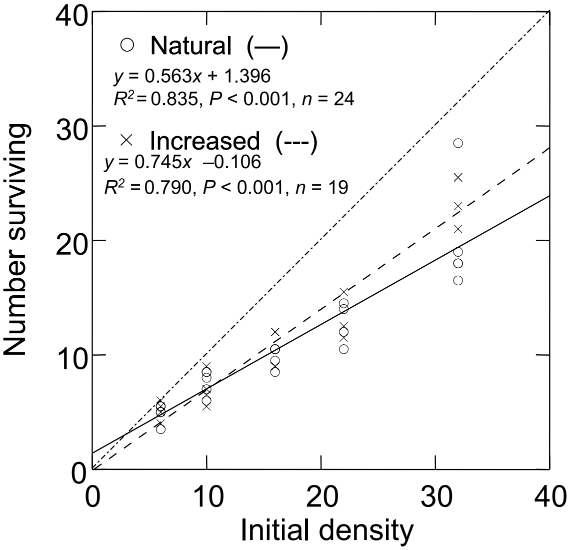

FIGURE 2. Number of grasshoppers surviving at five densities (no./m^2) with increased or natural food resources. Lines and equations are from regression analysis. A line with a slope of one is provided as a reference point.

and grasshopper density was not significant (Table 1). Although positively related, per capita digestible biomass explained only 18% of the variation in proportional survival in the increased resource treatment ($y = 0.186x + 0.642$, $R^2 = 0.180$, $P = 0.04$, $n = 19$) and 34% of the variation in the natural resource treatment ($y = 1.018x + 0.576$, $R^2 = 0.340$, $P = 0.002$, $n = 23$) based on linear regression.

Reproductive allocation

Egg production (follicular relicts) and per capita digestible biomass were positively and significantly related, with per capita digestible biomass explaining over 60% of the variation in egg production based on a linear regression (Fig. 3*a*). Egg production and percent digestibility of grass were positively related, with percent digestibility of grass explaining less than one-third of the variation in egg production ($y = 164.07x - 27.27$, $R^2 = 0.328$, $P = 0.001$, $n = 29$). Functional ovariole number was positively associated with per capita digestible biomass (Fig. 3*b*), indicating that grasshoppers with higher per capita resource availability were producing larger egg pods when the experiment was terminated. Vitellogenesis and the proportion of initiated follicles completing egg development were also positively related to per capita resource availability (Figs. 3*c*, 3*d*). Both increased grasshopper density and natural resource availability negatively affected the number of eggs laid as measured by follicular relicts (Table 1). The residuals from the regressions of egg production did not differ between resource (ANOVA, MS = 24.2, $F_{1,27} = 0.41$, $P = 0.53$) or density treatments (ANOVA, MS = 89.7, $F_{4,24} = 1.72$, $P = 0.18$). In addition, the residuals from the regressions of vitellogenesis did not differ between resource (ANOVA, MS = 38.7, $F_{1,27} = 0.44$, $P = 0.51$) or density treatments (ANOVA, MS = 110.2, $F_{4,24} = 1.34$, $P = 0.28$). The CV of the number of eggs laid (follicular relicts) was significantly higher in the natural resource treatment than in the increased resource treatment (Table 1). In the natural resource treatment, the CV of follicular relicts in the highest density treatment was significantly higher than in the second lowest density treatment (Table 1), whereas the

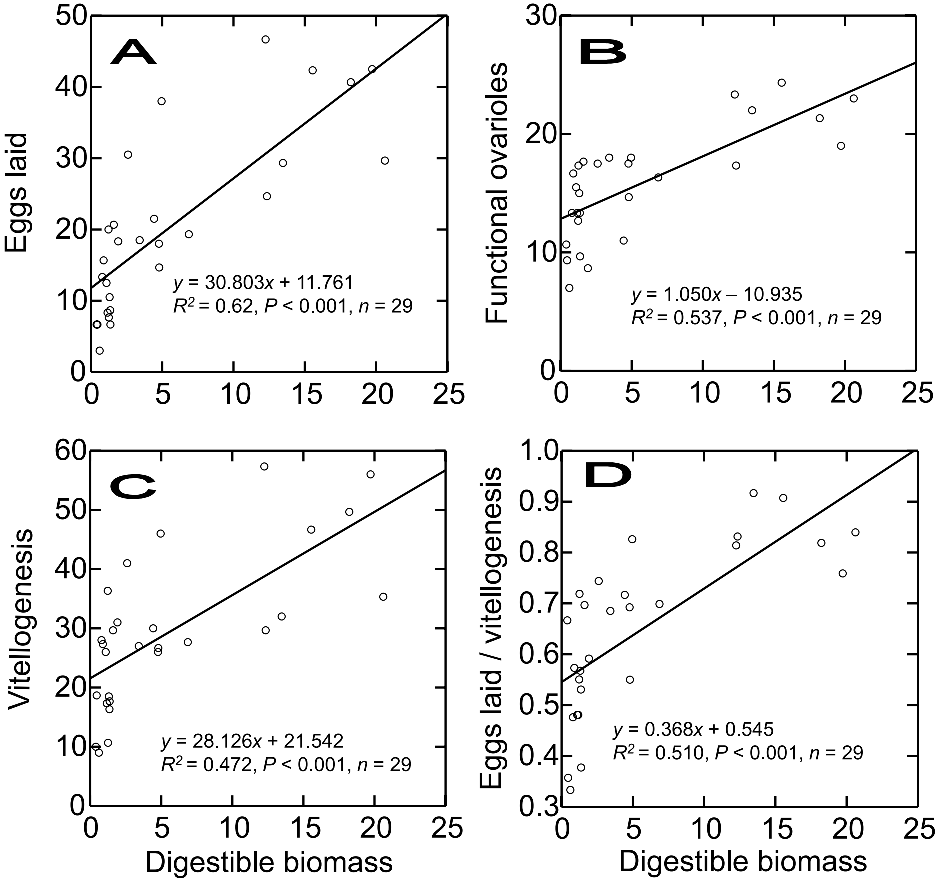

FIGURE 3. Per capita number of eggs laid (follicular relicts) (A), of functional ovarioles present (B), and of ovarioles initiating vitellogenesis (C) *versus* per capita digestible vegetation biomass (g dry/m^2 per no. of grasshoppers in a cage), and ratio of eggs laid to ovarioles initiating vitellogenesis *versus* per capita digestible vegetation biomass (g dry/m^2 per no. of grasshoppers in a cage). Lines and equations are from regression analysis.

CV in the highest density treatment showed a trend towards higher values than the lowest density treatment (Table 1).

Discussion

With strong density dependence solely in the form of egalitarian exploitative competition, survival should remain high until crashing at the point when individuals are unable to obtain the minimum resources required for survival (Nicholson 1954). In contrast, strong density dependence in the form of nonegalitarian scramble competition should result in population densities declining to similar final densities among the highest density treatments, resulting in lower proportional survival (Joern and Klucas 1993); however, populations did not crash and final densities did not converge to similar levels in the highest density treatments in either resource treatment even with initial densities approaching 90 grasshoppers per m^2. Although there was evidence for density dependence in proportional survival, per capita resource availability explained only 18 and 34% of the variation in proportional survival in the increased and natural resource treatments, respectively. In contrast, initial treatment densities explained over 80% of the variation in numbers surviving in both resource treatments. Although per capita resource availability was lower in the natural resource treatment, there was little indication of significant resource-limited survival, as the slopes of the regression lines did not differ between the resource treatments. The weak effects of density dependence on survival are in contrast to Joern and Klucas (1993) and Belovsky and Slade (1995), although Ritchie and Tilman (1992) found that high population densities of grasshoppers did not always lead to density-dependent competition, particularly in high biomass fertilized plots. The combination of abundant food in the environment and cool climatic conditions reducing metabolic requirements likely contributed to the lack of strong density-dependent survival in this experiment.

Exploitative competition for resources was important, as per capita resource availability explained over 60% of the variation in egg production. Females with reduced per capita resource availability produced fewer eggs (follicular relicts), initiated fewer ovarioles (vitellogenesis), and completed development in a lower proportion of ovarioles that initiated development, which are all consistent with the expected effects of low resource availability (Chapman 1998). The positive relationship between functional ovariole number and per capita resource availability indicates that the effects of per capita resource availability persisted to the end of the experiment. Because both vitellogenesis and the ratio of eggs laid relative to vitellogenesis increased with per capita digestible biomass, the reduced egg production with lower per capita resource availability results from both a lower rate of ovariole initiation and a lower percentage of initiated ovarioles completing development. An increased ratio of eggs laid relative to vitellogenesis with increasing per capita resource availability has also been found in locusts (McCaffery 1975). Interference competition or other density-dependent factors do not appear to have large effects on reproductive allocation, as the regression residuals for egg production and vitellogenesis did not differ between density treatments. In a prior study in the Palouse prairie, there was little visual evidence of interference competition or antagonistic behavior observed (Belovsky and Slade 1995). Therefore, exploitative competition for resources probably had a primary role in determining reproductive allocation in *M. sanguinipes* females.

Melanoplus sanguinipes females increased mean reproductive allocation with per capita resource availability, and survival was not affected by resource availability. These results suggest that *M. sanguinpes* females could be trading off allocation to reproduction for maintenance, thereby increasing survival when resources are limiting (de Souza Santos and Begon 1987). Such a pattern would fit predictions from resource-allocation models that grasshoppers should increase proportional allocation to survival when current resource availability is low but future reproduction is possible (Branson 2001).

Although abundant digestible plant biomass remained in cages initiated at higher densities, grasshoppers still appeared to exploitatively compete for food. The percent digestibility of grass was lower in the highest density increased resource treatment than in the three lowest density increased resource treatments, and in both resource treatments was lower in the highest density treatment than in the vegetation control treatment. These results are consistent with grasshoppers selectively removing the highest quality portion of the available biomass, leading to exploitative competition for limited amounts of high-quality vegetation even though resources appeared abundant in the environment. Grasshoppers have been shown to selectively forage on the available plant tissue biomass to maximize survival and reproduction, with significant variation existing within and between plants in quality (Bernays and Chapman 1994).

Even in a year with high resource availability and cool temperatures, reproductive allocation and vitellogenesis of *M. sanguinipes* females increased with per capita resource availability. This indicates that *M. sanguinipes* females were food limited even though survival was not affected by resource availability. The level of food limitation did not lead to reduced survival at higher initial densities, although with stronger food limitation both survival and reproduction would likely decrease. In a study at the same area, Belovsky and Slade (1995) found stronger density-dependent effects on grasshopper survival than in this study, but the effectiveness of increased resources declined in years with greater precipitation. Their experiments were conducted in years with lower vegetative biomass and warmer abiotic conditions than in this study, which would increase food limitation and exploitative competition.

The cool abiotic conditions during the study, and shade from the abundant vegetation, likely reduced metabolic rates and limited the effectiveness of active thermoregulation to raise body temperatures (Willott 1997). Given the cool abiotic conditions during the study, *M. sanguinipes* females could have been constrained by their ability to process food instead of resource availability (Stephens and Krebs 1986). If this was the case, resource-acquisition rates should either be equal in all cages or differ between treatments if the quality of available vegetation differed in ways not detected by the acid–pepsin digestion method. Since the regression residuals for egg production and vitellogenesis did not differ by resource treatment, the combination of per capita plant biomass and acid–pepsin digestibility appears to have accurately assessed the quality of resources available for grasshopper performance. Although vegetation quality could be more important than biomass in determining grasshopper performance, the percent digestibility of grass explained less than one-third of the variation in egg production, much lower than that with per capita digestible biomass. Given the vegetation-sampling methods used, I was unable to address if grasshopper performance responded to a minimum level of plant quality. Therefore, the main effect of the density and resource treatments on reproductive allocation was most likely due to the variation in per capita digestible resource availability resulting from the treatments.

Individual variation in exploitative competitive ability affecting reproduction allocation has important implications for our understanding of life-history variation of organisms (Nylin and Gotthard 1998). Individual differences in exploitative competitive ability appeared to be important in determining egg production (follicular relicts) of individual *M. sanguinipes* females. Because the CV of egg production was higher in the natural resource treatment and in the highest density treatment, the variation among individuals in eggs produced appeared to increase with low per capita resource availability. Thus, some of the decrease in mean egg production with increasing density results from differential performance among individuals and not from consistent reductions among all individuals. Exploitative resource competition was likely stronger when per capita resource availability was low, leading to increased variation in performance between individuals with differing abilities to exploit resources. Based on residual analysis, the increased variance in egg production among individuals likely resulted from exploitative competition and not interference competition. Additional experiments would be required to determine if the mean values accurately assessed changes in reproductive allocation of individuals. It may be inaccurate to examine the predictions of optimal allocation models using mean values of multiple individuals, as discussed above, when differences among individuals are important.

Conclusion

Melanoplus sanguinipes grasshoppers allocated resources to reproduction in response to per capita resource availability, even in a year with high natural resource availability and cool temperatures. These results indicate that density-dependent factors and the effects of climate on food quality and availability were of primary importance in determining future population dynamics. This study demonstrates that exploitative competition for resources can have important effects on population dynamics even when resources appear abundant in the environment. Both individual and population-level responses appear important in understanding reproductive allocation responses to resource availability and intraspecific density, but the results at both levels were consistent with the effects of exploitative competition. Interference competition did not appear to be important. More research is needed to assess the importance of *M. sanguinipes* individual variation in understanding the evolution of grasshopper life-history variation. Density dependence in reproduction was important even though effects on survival were small; as a result, assessment of population-level responses of reproductive allocation in response to resource limitation is required to more accurately predict grasshopper population dynamics and future outbreaks. Although nymphal survival in the year following high grasshopper populations can play an important role in population dynamics (Joern and Gaines 1990), these results suggest a large portion of the change in future population densities may be driven by failure of recruitment resulting from reduced reproduction. A better knowledge of the population dynamics of pest grasshopper species will also aid in the development of grasshopper management tools that use natural biotic processes (Joern 2000).

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