

Influence of a Large Late Summer Precipitation Event on Food Limitation and Grasshopper Population Dynamics in a Northern Great Plains Grassland

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ABSTRACT The complex interplay between grasshoppers, weather conditions, and plants that cause fluctuations in grasshopper populations remains poorly understood, and little is known about the ecological processes that generate grasshopper outbreaks. Grasshopper populations respond to interacting extrinsic and intrinsic factors, with yearly and decadal weather patterns and the timing of precipitation all potentially important. The effects of initial and increasing grasshopper densities on grasshopper survival and reproductive correlates were examined at a northern mixed-grass prairie site through manipulations of grasshopper densities inside 10-m² cages. High-quality grass growth occurred after a 9.1-cm mid-August rain. Reduced proportional survival was apparent in the two higher density treatments before the rain, indicative of food-limited density-dependent mortality. However, the large late summer rainfall event mediated the effects of exploitative competition on demographic characteristics because of the high-quality vegetation growth. This led to weaker effects of food limitation on survival and reproduction at the end of the experiment. The results indicate a direct link between weather variation, resource quality and grasshopper population dynamics led to a severe grasshopper outbreak and show that infrequent large precipitation events can have significant effects on population dynamics. Additional research is needed to examine the importance of infrequent large precipitation events on grasshopper population dynamics in grassland ecosystems.

KEY WORDS food limitation, grasshoppers, insect population dynamics, precipitation, weather conditions

Grasshoppers are an important component of grassland ecosystems in the United States and make a number of positive contributions to grassland health (McEwen 1987, Belovsky and Slade 2000, Branson et al. 2006). However, widespread economically damaging grasshopper outbreaks in western North America tend to occur cyclically at 8- to 10-yr intervals, with localized infestations occurring every year (Belovsky 2000, Branson et al. 2006). Grasshopper populations respond to a combination of interacting extrinsic (e.g., weather conditions) and intrinsic (e.g., biotic interactions) factors that vary spatially and temporally (Belovsky and Joern 1995, Joern 2000, Branson et al. 2006, Jonas and Joern 2007). The direct, indirect, and interacting effects weather conditions, host plants, grasshopper population densities, and other biotic factors have on grasshopper population fluctuations remain poorly understood (Lockwood 1997, Joern 2000, Fielding 2004, Branson et al. 2006, Jonas and Joern 2007). In addition, little is known about the ecological processes that generate grasshopper outbreaks (Lockwood 1997, Joern 2000, Branson et al. 2006), with few

experiments conducted while densities are increasing before an outbreak.

Extrinsic factors such as weather variation can directly and indirectly affect grasshopper population dynamics (Joern 2000, Branson et al. 2006, Jonas and Joern 2007, Powell et al. 2007). Yearly and decadal time scale weather patterns, as well as the timing of precipitation within a year, can positively or negatively impact grasshopper densities and influence community composition (Jonas and Joern 2007, Powell et al. 2007). In the northern Great Plains, spring precipitation is typically associated with lower grasshopper populations (Powell et al. 2007), although direct correlations between densities and climatic variables typically explain <30% of the variation in densities in western North America (Joern 2000). Density-independent mechanisms cannot regulate population dynamics (Belovsky and Joern 1995), but weather conditions directly affect grasshopper metabolic processes, population dynamics, and species interactions (Yang and Joern 1994, Chase 1996, Joern 2000, Ritchie 2000, Ovadia and Schmitz 2004, Jonas and Joern 2007). Precipitation also indirectly affects grasshopper population dynamics by modifying habitat structure and host plant availability and quality

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(Belovsky and Joern 1995, Joern 2000, Branson 2003, Joern and Mole 2005). Host plant quality typically declines throughout the growing season, leading to low nitrogen content in rangeland grasses by late summer (Belovsky and Slade 1995, Oedekoven and Joern 2000). Host plant nitrogen content and carbohydrate composition can limit grasshopper survival or reproduction (Joern and Behmer 1997, Joern and Mole 2005), with reproduction and survival most frequently positively related to nitrogen content and plant biomass in drier grassland systems (Joern and Behmer 1997, 1998; Ritchie 2000; Branson 2003).

Plant species and community responses to precipitation in many grassland ecosystems may be more closely related to the timing of precipitation or to individual rainfall events rather than the amount of annual precipitation (Knapp et al. 2002, Heitschmidt et al. 2005, Swemmer et al. 2007). Large rainfall or pulse precipitation events have important effects on population and ecosystem processes (Golluscio et al. 1998, Hjelle and Glass 2000, Chesson et al. 2004, Schwinning and Sala 2004), particularly in grasslands with lower annual precipitation levels (Knapp et al. 2002). In addition, global climate change is predicted to result in increased variability and more frequent extreme precipitation events (Easterling et al. 2000, Jentsch et al. 2007). Extreme weather events can result in large demographic responses in plants and animals, with single wet or dry years leading to population crashes or booms in a number of insect orders (Mattson and Haack 1987, Hawkins and Holyoak 1998, Easterling et al. 2000, Parmesan et al. 2000). However, the effects of intraseason variability in rainfall on insect populations remain poorly understood (Drake 2005). Site-specific experiments are required to move beyond pattern analysis and generate a mechanistic understanding of how large precipitation event affects population dynamics and ecosystem function (Swemmer et al. 2007).

Intra- and interspecific exploitative competition can also be important in determining the population dynamics of rangeland grasshoppers (Ritchie and Tilman 1992, Joern and Klucas 1993, Chase and Belovsky 1994, Belovsky and Slade 1995, Evans 1995), although the importance of resource limitation changes with predation and environmental conditions (Belovsky and Joern 1995). Exploitative competition for resources can still exist under conditions of abundant plant biomass if high-quality food is limited (Joern and Klucas 1993, Joern 2000, Branson 2003). Nymphal resource availability affects nymphal mortality rates (Danner and Joern 2003) but does not directly affect the reproduction of individuals that survive to adulthood (Branson 2004). Importantly, food limitation for adults may initially have stronger effects on grasshopper reproduction than survival (Branson 2003, 2006).

Experimental manipulations of grasshopper populations are useful in examining mechanisms responsible for grasshopper population fluctuations and outbreaks, because population densities and other factors can be manipulated at a single site (Kemp 1992, Belovsky and Joern 1995, Belovsky and Slade 1995, Bran-

son et al. 2006). Small scale cage experiments can also provide insights into processes operating at larger scales (Belovsky and Joern 1995, Schmitz 2004). More knowledge on grasshopper population dynamics is needed to aid in the development of management approaches that attempt to reduce grasshopper outbreaks through the manipulation of ecological interactions rather than with chemical pesticides (Branson et al. 2006). In this experiment, the effects of initial and increasing grasshopper densities on grasshopper population dynamics, reproductive correlates, and rangeland vegetation were examined at a northern mixed-grass prairie site by manipulating grasshopper densities inside 10-m² cages.

Materials and Methods

The experiment was conducted in 1999 at the USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT, in a mixed-grass prairie highly dominated by western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve, also called *Agropyron smithii*]. Blue grama [*Bouteloua gracilis* (Willd. ex Kunth Lag. ex Griffiths)] was also present. Field brome (*Bromus arvensis* L., also known as Japanese brome) occurred at the site but had senesced before the start of the experiment. On average, >90% of annual vegetation production occurs by 1 July when the experiment was initiated (Heitschmidt and Vermeire 2005). Midsummer grasshopper densities at a site within 2 km ranged from 8 to 17/m² in 1997, 13 to 31/m² in 1998, and 10 to 45/m² in 1999. (D.H.B. and J. Onsager, unpublished data). Peak grasshopper densities in the close vicinity of the site ranged between ≈15 and 130/m² between 1999 and 2001 (Branson 2005).

The effect of initial and increasing grasshopper densities on survival, body size, and reproductive correlates were examined by manipulating grasshopper densities in 10-m² insect cages. The cages were constructed of Lumite (SI Corp., Gainesville, GA) insect screening with 15-cm-wide polyester flaps at the base that laid flat around the exterior of the cage. Zippers on two sides and in corners allowed access. The cages were placed over a frame composed of electrical conduit and fastened to the ground with spikes driven through grommet holes in the flaps. Sandbags were placed continuously around the cage on the flaps to prevent grasshoppers from escaping. Cages have been used in numerous studies with grasshoppers (Joern and Klucas 1993, Belovsky and Joern 1995, Belovsky and Slade 2000, Schmitz 2004).

The five treatments examined were field density, reduced density, increased density, immigration, and vegetation control. Field density cages were initiated at a density of 25 grasshoppers/m², which was the approximate density of grasshoppers in uncaged control plots at the time the experiment was initiated. Reduced density treatment cages were initiated at ≈50% of the field density, whereas increased density treatment cages were initiated at ≈150% of the field density. Immigration treatment cages were initiated at

the field density and were designed to examine the effects of increasing food limitation on grasshopper survival and reproduction. Every 7–10 d beginning on 9 July, a number of grasshoppers equivalent to 10% of the field density at the site over a 10-m² area were added to immigration treatment cages. Grasshoppers were randomly caught at the site to ensure the taxonomic composition of grasshoppers added approximated that of the site. Grasshoppers added to the immigration treatment were marked by removing one antenna, to allow reproductive analyses to be conducted on individuals present throughout the experiment. The cumulative addition to the immigration treatment throughout the experiment was 23.5 grasshoppers/m², with no individuals added during the last 10 d of the experiment. All grasshoppers were removed from vegetation control cages at the start of the experiment to assess the effects of grasshopper herbivory on vegetation. Treatments were randomly assigned to cages, with four replicates per treatment.

After cages were installed, an initial assessment of grasshopper densities was conducted on 1 July by counting the number of grasshoppers within eight 0.1-m² aluminum wire rings in each cage and in five 10-m² control plots adjacent to the cage site (Onsager and Henry 1977). Densities in cages were adjusted to the desired treatment densities by adding or removing grasshoppers. Grasshoppers added to cages were randomly caught at the site. Grasshopper densities were assessed approximately every 7–10 d from 15 July to 15 September. In association with each density assessment, a random catch sweep net sample, consisting of a minimum of 150 fast sweeps in the grass canopy and 150 slow sweeps at ground level, was taken in the vicinity of the site to establish grasshopper community composition and development (Berry et al. 2000). Both fast and slow sweeps were used to reduce potential sampling biases resulting from movement abilities or habitat preferences of grasshoppers (Larson et al. 1999). Random catch samples were frozen for later identification to species and developmental instar. Grasshopper species composition at the site was comprised of 55% *Phoetaliotes nebrascensis* (Thomas), 24% *Melanoplus sanguinipes* (Fabricius), 11% *Ageneotettix deorum* (Scudder), 5% *Opeia obscura* (Thomas), and 5% other species, averaged across multiple random catch samples. The four most common grasshopper species all feed on grasses, although *M. sanguinipes* is a highly polyphagous species that also feeds on a wide range of forbs (Pfadt 2002). On 1 July when the experiment was initiated, >70% of *M. sanguinipes* in a random catch sample were fourth- or fifth-instar nymphs, with no first- or second-instar nymphs. *P. nebrascensis* grasshoppers were at an earlier developmental stage, with 30% first- and second-instar nymphs and only one fourth-instar nymph.

At the end of the experiment in mid-September, all observed grasshoppers were removed from cages using insect nets. This process was repeated three times over 2 d for each cage. All grasshoppers were immediately frozen for later identification and reproductive

analyses. Ovary analysis was used to determine the proportion of functional ovarioles in five females of *M. sanguinipes* and *P. nebrascensis* in each cage (Joern and Klucas 1993, Branson 2003, 2006). Grasshopper ovaries consist of a series of ovarian follicles, which are typically not all functional or developing (Bellinger et al. 1987, Joern and Gaines 1990, Branson 2003). Functional or developing, ovarian follicles (functional ovarioles) are an indication of the size of the next egg pod laid and are typically correlated with reproductive output (Uvarov 1966, Branson 2003).

Vegetation at the site was sampled every 7–10 d from July through early September by randomly tossing ten 0.1-m² rings in untrampled areas directly surrounding the cage site. All vegetation was clipped in each plot to assess standing green biomass and percentage total nitrogen content of green grass. After grasshoppers were removed from the cages in mid-September, five plots in all cages and control plots were clipped in a similar fashion. Green vegetation was separated by grasses and forbs, dried, weighed, and ground using a Wiley mill (Belovsky and Slade 1995). The percentage total nitrogen content of green grass samples was assessed using a dry combustion C/N analyzer (Matejovic 1997) and was used as a measure of host plant quality. Treatment differences in forb biomass were not examined because of the limited forb biomass in most samples.

Proportional survival was assessed over two separate time periods during the experiment. Proportional survival was used to assess the importance of density-dependent mortality, because treatments were initiated with differing initial population densities. Treatment differences in the density of grasshoppers removed from cages at the end of the experiment were also analyzed. On 11 August, a 9.1-cm rainfall event occurred at the site, which led to vegetative regrowth and sprouting of *Bromus* seedlings. To determine whether the large late summer rainfall event reduced food limited mortality, separate analyses were conducted to examine proportional survival from the beginning of the experiment until the 9.1 cm of rain and from the precipitation event to the end of the experiment. Proportional survival before the rainfall event was calculated by dividing the mean density value from two counts nearest the rainfall event by the mean of the two initial ring counts. Proportional survival after the rainfall was calculated by dividing the mean of the final two ring counts by the mean of the two counts nearest the rainfall event. The mean of two ring counts were used in all proportional survival analyses to reduce the effects of random sampling error caused by sampling in only eight rings per cage (Berry et al. 2000). As grasshoppers were added to the immigration treatment, the density of grasshoppers added over the first or second time period was combined with the initial or midpoint density to serve as the dividend in proportional survival calculations. Separate multivariate analysis of variance models (MANOVAs) were used to assess overall treatment effects on vegetation characteristics, as well as grasshopper survival, density, and reproductive correlates. If a MANOVA model

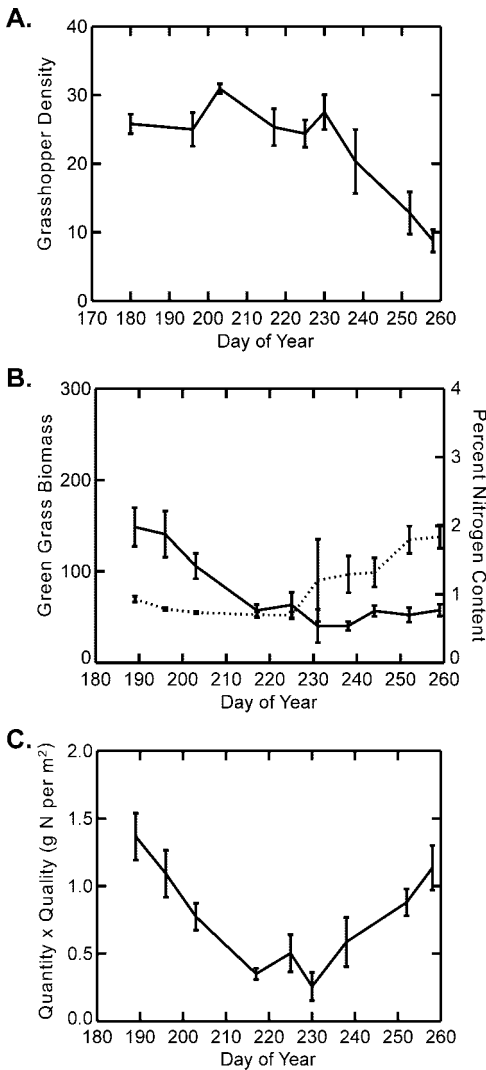


Fig. 1. (A) Grasshopper densities (\pm SE) per square meter in uncaged control plots over the course of the summer. (B) Green grass biomass (g dry/m², \pm SE) (—) and percentage total nitrogen content of green grass biomass (····) in random vegetation ring clips. (C) Protein availability (biomass \times quality) in green grass biomass (g N/m², \pm SE). The 9.1 cm of rain occurred on day of year 223 (11 August).

was significant, univariate analyses of variance were used to assess treatment differences for vegetation characteristics, final grasshopper densities, proportional survival, and the proportion of functional ovarioles. Pearson correlations were used to examine the relationship between vegetation characteristics and the final or cumulative density of grasshoppers. Cage mean values were used as replicate values for all survival, reproduction, and vegetation analyses. Proportional data were arcsine square root transformed as necessary to normalize values (Quinn and Keough 2002). SYSTAT 11 (Systat Software 2004) was used for all statistical analyses.

Table 1. Statistical results of MANOVA model on green grass biomass, percent nitrogen content of grass, and grams of nitrogen in grass biomass per square meter (biomass \times quality)

MANOVA	Source	df	Wilks' lambda	F	P
Univariate F test for Grass biomass	Treatment	12,34	0.0461	6.36	<0.0001
	Error	15	158.8		
Percent nitrogen content	Treatment	4	0.386	5.40	0.007
	Error	15	0.072		
Grams N per square meter	Treatment	4	0.0018	21.42	<0.001
	Error	15	0.001		

Percentage data were arcsine square root transformed before analysis to meet normality assumptions.

Results

Grasshopper densities in uncaged controls remained relatively stable throughout much of the summer until declining in late August (Fig. 1A). Green grass biomass present in random vegetation clips in the vicinity of the cage site declined until mid-August, when biomass stabilized after 9.1 cm of rain on 11 August (Fig. 1B). The percent total nitrogen content was relatively stable until after the rainfall event (Fig. 1B). The high sample variation in nitrogen content evident immediately after the rain (day of year 231; Fig. 1B) resulted from grass regrowth and sprouting. The average percent total nitrogen content in green grass from random clips doubled during the last half of the experiment (Fig. 1B), with protein availability also increasing (Fig. 1C). Densities in control plots continued to decline when protein availability increased (Fig. 1, A and C).

The treatments significantly affected vegetation characteristics, based on a multivariate analysis (Table 1). Grasshopper herbivory significantly and negatively affected grass biomass at the end of the experiment, because all treatments with grasshoppers had reduced biomass compared with vegetation controls (Table 1; Fig. 2A). There was a trend for higher grass biomass in the decreased density treatment than in either the immigration or increased density treatments, with grass biomass \approx 45% lower in the two higher density treatments (Fig. 2A). The percentage nitrogen content present in green grass at the end of the experiment was significantly higher in the immigration and increased density treatments than in the vegetation control treatment (Table 1; Fig. 2B). Despite the higher green grass nitrogen content in the immigration and increased density treatments, all treatments with grasshoppers had a lower availability of protein (g N/m²) compared with the controls (Table 1; Fig. 2C). Protein availability per square meter declined with increasing densities, with a higher availability of protein in decreased treatment cages relative to immigration or increased density treatments, and in the field density treatment relative to the increased density treatment (Fig. 2C). As a result, higher densities of grasshoppers reduced both grass biomass and the

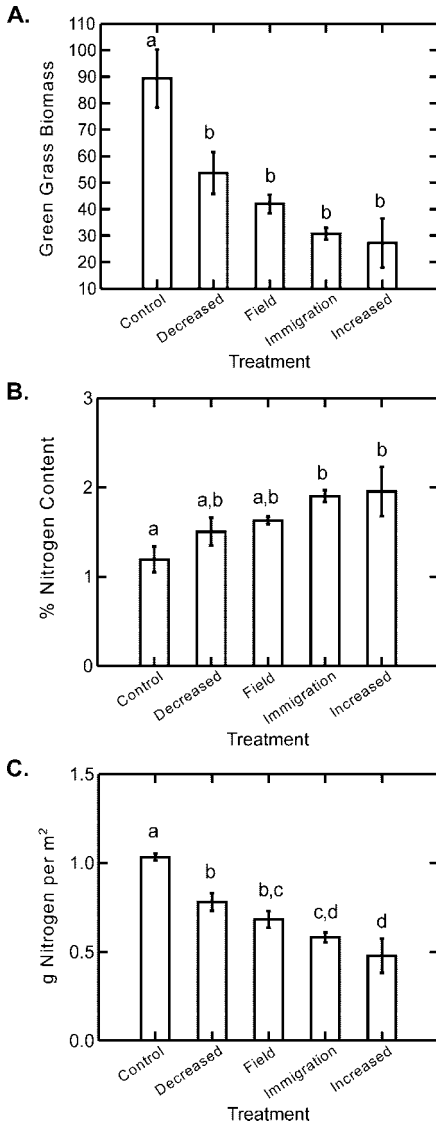


Fig. 2. (A) Green grass biomass (g dry/m², \pm SE) at the end of the experiment in each treatment. (B) Percentage nitrogen content of green grass biomass at the end of the experiment (\pm SE). (C) Protein availability (g N/m²) at the end of the experiment in each treatment (\pm SE). Treatment means with different letters are significantly different (Tukeys HSD with protected *P* values, *P* < 0.05).

overall availability of protein but resulted in a higher nitrogen content in the grass biomass that remained in cages. Correspondingly, nitrogen content and grass biomass were strongly negatively related to each other (Pearson correlation = -0.950 ; *P* < 0.001).

Density treatments significantly affected survival and reproductive correlates, based on a multivariate analysis (Table 2). Proportional survival measured from the beginning of the experiment until the rainfall event differed significantly between treatments (Table 2), with lower proportional survival in immigration

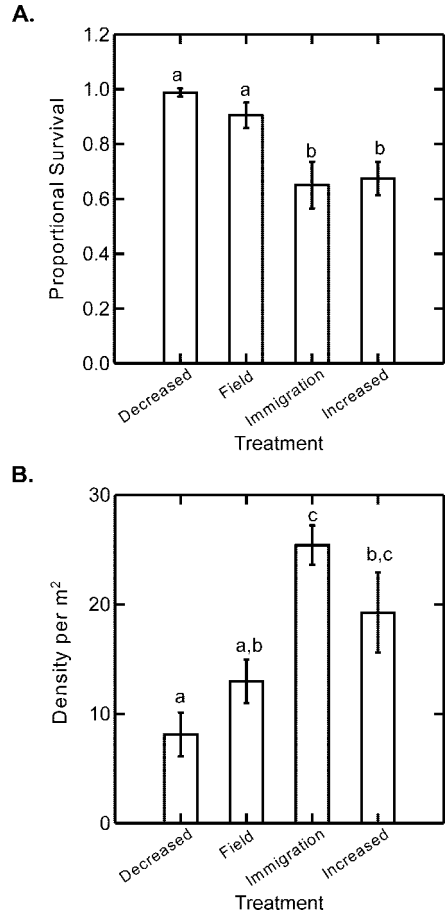


Fig. 3. (A) Proportional survival by treatment from the beginning of the experiment until the 11 August rain (\pm SE). (B) Density of grasshoppers per square meter removed from treatment cages at the end of the experiment (\pm SE). Treatment means with different letters are significantly different (Tukeys HSD with protected *P* values, *P* < 0.05).

and increased density treatments than in decreased and field density treatments (Fig. 3A). However, proportional survival during the second half of the experiment did not differ significantly between treatments (Table 2). The density of grasshoppers at the end of the experiment differed significantly between treatments, with a higher density in increased density and immigration treatment cages than in decreased density cages (Table 2; Fig. 3B). Pearson correlations were used to examine whether biomass or protein availability helped explain the final or cumulative density. For cages with grasshoppers, the density of grasshoppers present at the end of the experiment was negatively related to green grass biomass remaining in cages (Pearson correlation = -0.501 ; *P* = 0.048) but only marginally negatively related to protein availability (Fig. 4A; Pearson correlation = -0.461 , *P* = 0.078). Grasshopper days, the cumulative abundance of grasshoppers throughout the experiment based on ring counts, was also negatively related to protein

Table 2. Statistical results from MANOVA model on proportional survival in the first and second half of the experiment (before and after new grass growth), density of grasshoppers removed from cages, and the proportion of functional ovarian follicles in *M. sanguinipes* and *P. nebrascensis* females

MANOVA	Source	df	Wilks' lamda	F	P
	Treatment Factor	15,19	0.0195	4.16	0.002
Univariate F test for					
Proportional survival first half	Treatment	3	0.2511	11.06	0.001
	Error	11	0.023		
Proportional survival second half	Treatment	3	0.072	1.45	0.282
	Error	11	0.049		
Density of grasshoppers at the end of the experiment	Treatment	3	229.68	13.98	<0.001
	Error	11	16.43		
Proportion of functional ovarian follicles in <i>M. sanguinipes</i> females	Treatment	3	0.0233	3.91	0.04
	Error	11	0.0059		
Proportion of functional ovarian follicles in <i>P. nebrascensis</i> females	Treatment	3	0.0187	7.36	0.006
	Error	11	0.0025		

Proportional data were arcsine square root transformed before analysis to meet normality assumptions.

availability (Fig. 4B; Pearson correlation = -0.58; $P = 0.02$).

The proportion of functional ovarian follicles in *M. sanguinipes* females differed significantly between treatments (Table 2), with a lower proportion of functional ovarioles in the immigration than in the de-

creased treatment (Tukey's HSD, $P < 0.05$). The proportion of functional ovarioles in *P. nebrascensis* females also varied significantly (Table 2), with a lower proportion of functional ovarian follicles in the increased treatment than in either the decreased or field density treatments (Tukey's HSD, $P < 0.05$). For both species, the average proportion of functional ovarioles was >70% in all treatments, leading to small relative differences between treatments in the number of functional ovarian follicles.

Discussion

In eastern Montana, peak current year grass biomass typically occurs between mid-June and mid-July and declines after that point (Heitschmidt et al. 1995, Heitschmidt and Vermeire 2005, Haferkamp et al. 2005), with nitrogen content and forage quality of grasses generally declining with the developmental stage (Heitschmidt et al. 1995). Nitrogen content of grasses doubled and green grass biomass stabilized during the last month of the experiment (Fig. 1B), resulting from new growth of western wheatgrass and field brome. This led to higher protein availability for foraging grasshoppers after the large rainfall event (Fig. 1C). However, grasshopper densities in control plots continued to decline when protein availability increased (Fig. 1, A and C). In a laboratory study, Joern and Behmer (1998) found the maximum rate of egg production occurred at $\approx 4\%$ nitrogen for both *P. nebrascensis* and *M. sanguinipes*, although survival of *P. nebrascensis* declined with nitrogen content. Average nitrogen content of random vegetation clips never exceeded 2% (Fig. 1B), but random clips are a coarse grained measure of nitrogen availability that cannot assess the full range of nitrogen available at the small scale used by foraging grasshoppers. Food quality at a nearby site was significantly higher in 1999 than in either 2000 or 2001, when the nitrogen content of grasses averaged between ≈ 0.75 and 1.2% in late season random vegetation clips (Branson 2005). In the same study, late season green grass biomass was higher

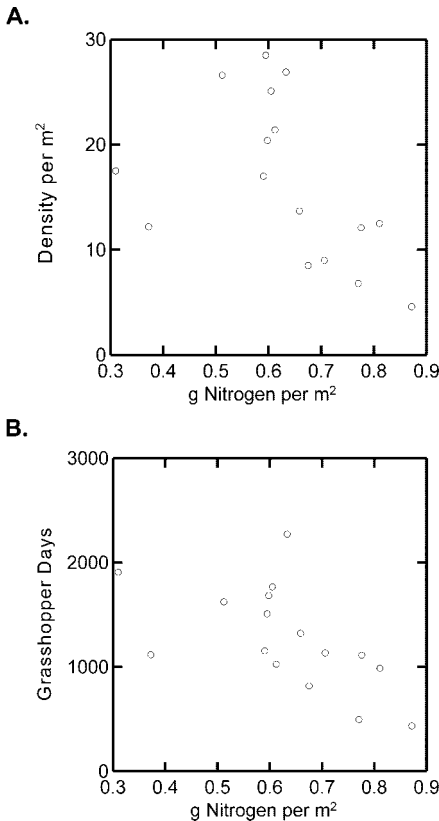


Fig. 4. (A) Scatterplot diagram of final grasshopper densities plotted versus protein availability (g N/m^2). (B) Scatterplot diagram of grasshopper days over the course of the experiment (ring density \times days) plotted versus protein availability (g N/m^2).

in 1999 than in 2000 but lower than in 2001 (Branson 2005).

Ritchie and Tilman (1992) argued that exploitative competition is likely to occur in situations where grasshoppers significantly reduce plant biomass relative to controls without grasshopper herbivory. In this experiment, herbivory significantly reduced grass biomass and protein availability in all treatments relative to the vegetative controls (Fig. 2, A and C). Although grass biomass did not differ significantly between density treatments, likely because of the low replication, a density-based resource response was evident in the amount of protein available per square meter (Fig. 2C). Furthermore, per capita resource availability in the increased and immigration treatment cages was much lower than apparent from Fig. 2, A and C, because more grasshoppers remained in these cages than in reduced or field density treatments (Fig. 3B). In contrast, nitrogen content of grass biomass present at the end of the experiment was positively associated with the level of grasshopper herbivory (Fig. 2B). Vegetation quality typically declines with increasing grasshopper densities or increased rates of herbivory, likely because of grasshoppers removing higher quality plant material (Chapman 1990; Redak and Capinera 1994; Branson 2003, 2006). Nitrogen content also typically declines monotonically with grass maturity throughout the growing season (Belovsky and Slade 1995, Heitschmidt et al. 1995, Oedekoven and Joern 2000). The higher levels of herbivory in the increased and immigration treatments likely led to the removal of a greater proportion of older plant material, before higher-quality vegetation growth began after the large rainfall event. As a result, young plant material with higher nitrogen levels would have comprised a greater proportion of standing vegetation in the immigration and increased density treatments than in the reduced density treatment. The strong negative correlation between grass biomass and nitrogen content of grasses ($r = -0.95$) and the density-based response in protein availability (Fig. 2C) support this contention.

Strong density dependence in the form of resource-based exploitative competition should result in lower proportional survival in treatments with higher initial population densities (Joern and Klucas 1993). Additionally, grasshopper densities often decline to similar levels in treatments initiated above the food limited carrying capacity (Chase and Belovsky 1994, Belovsky and Slade 1995). Lower proportional survival occurred in both the increased density and immigration treatments relative to the decreased and field density treatments in the first half of the experiment (Fig. 3A), indicating that resource limitation led to exploitative competition. Resource limitation seemed to be weaker after the late summer vegetation growth, because proportional survival during the second half of the experiment did not differ between treatments (Table 2). The density of grasshoppers in the increased density treatment did not converge with that of the field density treatment by the end of the experiment (Fig. 3B), as would be expected if initial densities were above the food limited carrying capac-

ity in both treatments. The trajectory of densities in the increased density treatment visually appeared to decline by approximately one third before the rainfall event, before stabilizing until the last week of the experiment. Protein availability was only marginally negatively correlated with the density of grasshoppers removed from cages (Fig. 4A), likely a result of the high-quality late season regrowth. Taken together, these results indicate that density-dependent effects on survival were not as strong during the second half of the experiment when new plant growth occurred. In a year when vegetation quantity and quality declined throughout the summer, as typically occurs in the northern Great Plains (Heitschmidt et al. 1995, 2005), the food limitation evident in higher-density treatments during the first half of the experiment would likely persist or strengthen leading to stronger exploitative competition and density-dependent mortality.

Even when density-dependent mortality is not apparent, resource limitation can strongly affect reproduction in grasshoppers (Branson 2003, 2006). With significant exploitative competition, females in treatments with higher densities would be predicted to have proportionally fewer functional ovarioles, leading to reduced egg pod sizes (Branson 2003). A lower proportion of ovarian follicles were functional for *M. sanguinipes* in the immigration treatment and for *P. nebrascensis* in the increased density treatment relative to the reduced or field density treatments. However, a high proportion of ovarian follicles were functional in all treatments, and the effects of increased densities were inconsistent between species. In comparison, the proportion of functional ovarian follicles in *M. sanguinipes* and *P. nebrascensis* females from random catch samples was 50% lower in 2000 than in 1999 (D.H.B., unpublished data). When viewed in the context of previous studies (Belovsky and Slade 1995, Branson 2003, 2004, 2006), the results are indicative of relatively weak exploitative competition at the end of the experiment. The timing of the increased late season resource availability in relation to the initiation of reproduction could also have important consequences, especially as it relates to egg pod size (Moehrlin and Juliano 1998). Assuming minimal direct residual effects of nymphal food limitation on reproduction as found by Branson (2004), females of both species likely either reproductively responded to the increased resources or began encountering sufficient food as ovarioles were developing. Some females of the earlier developing *M. sanguinipes* were present 3 wk before the rainfall. With a prereproductive diapause of 2–3 wk (Pfadt 2002), females of the later developing *P. nebrascensis* may have begun to encounter higher quality food as ovarioles were developing.

Viewed from a population dynamics perspective, small reductions in egg pod size with increasing population density would likely lead to relatively small effects on future population dynamics. Grasshopper densities in both the increased and immigration treatments were more than double those in the reduced density treatment at the end of the experiment (Fig. 3B), whereas mean

treatment differences in the proportion of functional ovarioles were $<15\%$. As a result, the total number of eggs laid was likely much greater in increased density treatment cages relative to reduced or field density treatment cages, assuming a similar per capita number of egg pods across treatments as expected with weak resource limitation (Branson 2004). Peak grasshopper densities reached $\approx 130/\text{m}^2$ at the site in the following year, a further indication that the availability of high-quality late season vegetation reduced food limitation and enhanced the reproduction of surviving females. Therefore, it seems a primary contribution of a large late season rainfall event on grasshopper population dynamics resulted from the availability of high-quality vegetation enhancing reproduction. Likely because of their later phenology, *P. nebrascensis* seemed better able to reproductively respond to the increased late season food availability, increasing from 55 to 78% of random catch samples in 2000.

Although the increased availability of protein late in the experiment led to an apparent reduction in exploitative competition inside cages, grasshopper densities in control plots continued to decline as protein availability increased (Fig. 1A). There are a number of potential explanations for the lack of tightly synchronized dynamics between cages and outside controls. It seems populations inside cages declined more rapidly before the large rainfall event than in the outside controls, based on a visual analysis of population trajectories. This would result in higher per capita food availabilities inside cages after the vegetation regrowth. A large reduction in the density in the increased treatment cages over the last sampling period is indicative of a delayed effect of food limitation inside cages. The possibility of confounding cage effects on microclimate or grasshopper emigration from control plots cannot be discounted. Although the timing of the dynamics differed, the reproductive response of grasshoppers to the rainfall event was evident in both cages and outside controls where densities reached $\approx 130/\text{m}^2$ in the following year.

Numerous biotic and abiotic factors can affect grasshopper population dynamics (Belovsky and Joern 1995, Joern 2000). Although the use of insect cages excluded avian predators that can regulate grasshopper population densities (Belovsky and Joern 1995), there was no effect of avian predation on late summer grasshopper densities at the site in 1999 (Branson 2005). This indicates that avian predation acted largely in a compensatory fashion (Branson 2005). Previous studies finding avian limitation of grasshopper populations have occurred with relatively low grasshopper densities (Belovsky and Joern 1995). Higher late summer temperatures would provide increased opportunities for grasshoppers to assimilate the higher-quality grass available in late summer and consequently result in higher reproduction and survival rates relative to cooler years (Yang and Joern 1994, Willott and Hassall 1998, Branson 2003). However, mean temperatures during August were similar to the long-term average and mean September temperatures were $\approx 4^\circ\text{C}$ cooler than the long-term average (Western Regional Climate Center).

Easterling et al. (2000) argued that important biotic responses could result from both longer-term weather patterns and brief extreme events, although extreme weather events have received limited attention in population ecology (Jentsch et al. 2007). The vegetation dynamics observed during this study do not occur on a regular basis in the northern Great Plains (Heitschmidt and Vermeire 2006, Heitschmidt et al. 1995, 1999, 2005), because large late season rainfall events that would create adequate soil moisture for late summer grass growth and germination are uncommon (Heitschmidt and Vermeire 2005, 2006). Based on long-term weather data at the Frank Wiley Airport, located <15 km from the site, the probability of 7.6 cm of precipitation occurring during the entire month of August is $<10\%$ (Western Regional Climate Center). Although the weather conditions during this study are not likely to be a frequent occurrence, in a nearby study examining drought effects on vegetation production and quality, the nitrogen content of both western wheatgrass and warm season grasses increased with mid-July and August precipitation (Heitschmidt and Vermeire 2006). As a result, the observed vegetation responses would be expected to occur after large late summer rainfall events in the northern Great Plains.

Little is known about the development of grasshopper outbreaks (Lockwood 1997, Joern 2000, Branson et al. 2006). Logan et al. (2006) speculated that extreme rainfall events or years with above normal food quality could play an important role in grasshopper population dynamics, but the effects of large or extreme rainfall events on grasshopper population dynamics have received little attention (Powell et al. 2007). In this study, the effects of exploitative competition were mediated by the effects of late summer precipitation on food availability, leading to weak effects of resource limitation even in treatments where densities were $>30/\text{m}^2$ for much of the experiment. Densities in outside controls were over four times higher the following year, resulting in a severe grasshopper outbreak with peak nymphal densities approaching $130/\text{m}^2$. Thus, the origin of an outbreak can be traced to the availability of high-quality grass biomass after a large late summer rainfall event, which led to high rates of survival and reproduction. Both the timing of precipitation and longer-term weather patterns seem important for understanding grasshopper population dynamics. Powell et al. (2007) found lower populations associated with years with high spring precipitation, whereas Ovadia and Schmitz (2004) found a negative association between yearly rainfall and grasshopper survival. Jonas and Joern (2007) showed that decadal scale weather processes can also play an important role in determining grasshopper species composition and abundance. Additional research is needed to examine the complex interplay between extrinsic and intrinsic factors on grasshopper population dynamics and species composition (Branson et al. 2006, Jonas and Joern 2007).

Jonas and Joern (2007) argued that the response of grasshoppers to precipitation is likely driven by trade-offs between plant quality, plant biomass, and other biotic factors. Although the weather conditions that led to the high population growth rate are uncommon, the

results are indicative of a direct link between weather variation, resource quality, and grasshopper population dynamics leading to a grasshopper outbreak (Joern 2000). Because this study examined grasshopper responses to a naturally occurring large late summer precipitation event in only a single year, strong generalizations regarding the effects of late summer precipitation on grasshopper population dynamics are not possible. The results indicate that infrequent large precipitation events can have important effects on grasshopper population dynamics and point to the need for additional manipulative experiments examining the effects of the timing and size of large precipitation events on grasshopper population dynamics in grassland ecosystems.

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