ABSTRACT Although most North American grasshopper species overwinter as eggs, some species hatch in late summer, overwinter as nymphs, and become adults in late spring. These species periodically reach outbreak densities, but it is unknown if they impact the population dynamics of later developing egg-overwintering grasshopper species. Two experiments were conducted in a northern mixed-grass prairie to examine the effects of herbivory by nymph-overwintering grasshoppers on survival of an egg-overwintering grasshopper, *Ageneotettix deorum*. When very high densities of nymph-overwintering grasshoppers reduced grass biomass by 80%, survival of *A. deorum* nymphs was significantly reduced. There was no effect of early season herbivory at a lower density of 16/m² on survival of *A. deorum* nymphs. The effects of early season herbivory appear consistent with exploitative competition. Although a strong reduction in peak grass biomass caused by early season herbivory negatively affected late season grass-feeding grasshopper densities, additional research is needed to examine the potential importance of early summer herbivory on population dynamics of later developing grasshoppers.

KEY WORDS grasshoppers, competition, Orthoptera, herbivory, phenology

Economically damaging grasshopper outbreaks in western North America occur frequently, but the processes that generate grasshopper outbreaks remain poorly understood (Lockwood 1997, Belovsky 2000, Joern 2000, Branson et al. 2006, Branson 2008). Exploitative competition frequently plays an important role in determining grasshopper population dynamics (Joern and Klucas 1993, Chase and Belovsky 1994, Belovsky and Slade 1995, Branson 2003), but the relative influence of biotic versus abiotic factors varies between years and sites (Belovsky and Joern 1995, Joern 2000, Branson et al. 2006, Branson 2008). A wide range of life history phenologies occur among the >400 grasshopper species in western North America (Pfadt 2002). Although most abundant pest species overwinter as eggs and hatch in early summer in central and northern North American grasslands, several nymph-overwintering species have largely offset phenologies. They hatch in late summer, overwinter as nymphs, and are adults by late spring (Pfadt 2002). These species periodically reach densities of >30 adults per square meter in early summer (Pfadt 2002, Foster et al. 2006, Brust et al. 2008; USDA–APHIS–PPQ, unpublished data), with fall nymphal densities as high as 140/m² (Foster et al. 2006).

Joern (2000) argued that research was needed to examine whether competition from noneconomic grasshopper species limits densities of economically important species. It is unknown if early season nymph-overwintering species impact the population dynamics of later developing egg-overwintering grasshopper species. Early season herbivory can positively or negatively affect later occurring species (Ohgushi 2005, Kaplan and Denno 2007). Competition has often been assumed to be less intense when herbivores feed at different times in the growing season (Denno et al. 1995, Ohgushi 2005, Kaplan and Denno 2007), but a recent review found similar competition effects on survival when phytophagous insects were temporally separated or co-occurred (Kaplan and Denno 2007). Exploitative competition can result from reductions in host plant biomass, whereas negative plant-mediated interactions can result from lower host plant quality or induced resistance. Belovsky et al. (2000) specifically hypothesized that earlier hatching grasshopper species could reduce survival of later hatching species through competition and reduce the likelihood of grasshopper outbreaks. Two experiments using different initial stocking densities were conducted at a northern mixed-grass prairie site in eastern Montana to examine the effects of early season herbivory by nymph-overwintering grasshoppers on nymphal survival of a later developing grasshopper species and graminoid biomass.

Materials and Methods

Site. Experiments were conducted in 2003 and 2004 at a northern mixed-grass prairie site in eastern Mon-
tana (47.47° N, 104.08° W). More than 90% of vegetative biomass is graminoids, with both cool (C3) and warm (C4) season grasses (Branson 2005). Graminoids included western wheatgrass (Pascopyrum smithii), blue grama (Bouteloua gracilis), needle and thread (Stipa comata), prairie junegrass (Koeleria pyramidata), and threadleaf sedge (Carex filifolia).

**Grasshoppers.** Eritettix simplex (Scudder) and Psoloessa delicatula (Scudder) were the dominant nymph-overwintering species at the site and were initiated in cages at approximately equal densities. Both species feed feed on sedges and cool season grasses in the spring and later switch to warm season grasses (Pfadt 2002). Ageneotettix deorum (Scudder), the egg-overwintering species examined, is widely distributed and often abundant in outbreaks (Pfadt 2002). It is also graminivorous (Mulkern 1967, Pfadt and Lavigne 1982). Adult nymph-overwintering grasshoppers and early-instar A. deorum overlap under field conditions. Because of high mortality rates associated with handling first- and second-instar nymphs and difficulties counting first- and second-instar nymphs in cages, experiments were initiated with third-instar A. deorum and examined only the effects of temporally separated competition.

**Experimental Protocol.** In both years, 0.25-m² cages were placed over areas with similar vegetation, avoiding areas of bare ground. Cages were constructed of Lumite (SI, Gainesville, GA) insect screening with 15-cm-wide polyester flaps at the base that laid flat around the exterior of the cage. The cages were placed over a frame composed of PVC water pipe and fastened to the ground with spikes. Sandbags were placed continuously around the cage on the flaps to prevent escapes. Similar cages have been used in numerous studies (Joern and Klucas 1993, Belovsky and Slade 1995, Schmitz 2004, Branson 2008). Experimental designs differed in densities of nymph-overwintering grasshoppers and A. deorum nymphs. For nymphal survival and peak biomass treatments, cages were initiated with a given density of nymph-overwintering grasshoppers or served as a control treatment with no grasshoppers. In 2003, cages were initiated with zero or four nymph-overwintering grasshoppers on 28 April. In 2004, cages were initiated with 0 or 15 grasshoppers on 5 May. Because some cages were damaged during the experiments or removed because of the presence of spiders, replication varied between five and seven cages for nymphal survival treatments. Peak biomass treatment replication was five cages in 2003 and four in 2004. Cages with nymph-overwintering grasshoppers were counted and restocked to the initial density twice within 2 wk of initiating the experiment to generate consistent treatment differences in early season herbivory before the addition of A. deorum.

Any surviving nymph-overwintering grasshoppers were removed from cages 24 June 2003 or 27 June, 2004. Nymphal survival treatment cages were initiated with third-instar A. deorum nymphs, using densities of 10 in 2003 and 20 in 2004. Cage counts assessed A. deorum survival but not the developmental stage of individual nymphs. The experiments were designed to examine the effects of nymph-overwintering herbivory on mortality of nymphal A. deorum and ended after ~3 wk, before nymphs molting to adults.

To examine the impact of early season herbivory on grass biomass, a 0.1-m² plot was clipped in peak biomass and control cages when nymph-overwintering grasshoppers were removed. Green vegetation was separated by grasses and forb, dried, weighed, and ground (Belovsky and Slade 1995). The percentage nitrogen content of green grass samples was assessed using a dry combustion C/N analyzer and used as an index of host plant quality. Forbs comprised <10% of total biomass and were not analyzed.

**Statistics.** t-Tests assessed treatment differences in survival, green grass biomass, and percentage nitrogen content. The number of grasshoppers alive in final two cage censuses was averaged before analysis to account for grasshoppers missed during counts. Percentage data were arcsine transformed before analysis. Systat 12 was used for all analyses (Systat Software 2007).

**Results**

Nymph-overwintering grasshoppers reduced peak grass biomass by ~30% relative to control cages without grasshoppers in 2003 (t-test: t = 2.330, P = 0.042; Fig. 1a). However, there was no effect of nymph-overwintering herbivory on grass nitrogen content (t-test: t = −0.370, P = 0.72; Fig. 1b). When initiated at 60/m² in 2004, nymph-overwintering herbivory reduced grass biomass by ~80% relative to controls (t-test: t = 7.703, P < 0.0001; Fig. 2a) but significantly and positively affected nitrogen content (t-test: t = −3.930, P = 0.004; Fig. 2b).

In 2003, herbivory by nymph-overwintering grasshoppers at a density of 16/m² did not significantly affect nymphal A. deorum percent survival (t-test: t = 1.34, P = 0.20; Fig. 1c) or the average number surviving (t-test: t = 1.32, P = 0.21, Fig. 1d). In 2004, nymph-overwintering grasshoppers were maintained at a higher density of 60/m², whereas A. deorum were initiated at 80/m². Prior herbivory by nymph-overwintering grasshoppers significantly reduced percent survival of A. deorum in 2004 (t-test: t = 3.06, P = 0.008; Fig. 2c) and the average number surviving (t-test: t = 3.09, P = 0.009; Fig. 2d). Therefore, detrimental effects of nymph-overwintering herbivory on nymphal A. deorum survival were evident only when densities simulated outbreak conditions for both nymph-overwintering grasshoppers and A. deorum.

**Discussion**

A better understanding of the impact of nymph-overwintering herbivory on peak grass biomass is needed, because ~360,000 acres of rangeland in Nebraska were sprayed in a skip swath approach in 2003 and 140,000 acres in 2004 in response to an outbreak of nymph-overwintering grasshoppers (USDA-APHIS-PPQ, unpublished data). Early season herbivory at a constant density of 16/m² significantly reduced forage availability by an average of 30%,
Fig. 1. (A) Green grass biomass (g dry/m²) in 2003. (B) Percentage nitrogen content of green grass biomass in 2003. (C) Percentage survival of *A. deorum* at 3 wk in 2003. (D) Average number of *A. deorum* surviving at 3 wk in 2003. Cages were initiated at zero and four nymph-overwintering grass-hoppers per 0.25-m² cage.

Fig. 2. (A) Green grass biomass (g dry/m²) in 2004. (B) Percentage nitrogen content of green grass biomass in 2004. (C) Percentage survival of *A. deorum* at 3 wk in 2004. (D) Average number of *A. deorum* surviving at 3 wk in 2004. Cages were initiated at 0 and 15 nymph-overwintering grasshoppers per 0.25-m² cage.
whereas an outbreak density of $80/m^2$ reduced forage availability by $\sim80\%$. Early season herbivory cages were maintained at a constant density to generate consistent herbivory before stocking A. deorum. Because densities of nymph-overwintering grasshoppers would naturally decline, higher peak field densities would be required to result in similar biomass reductions. Although the influence of early season herbivory on peak biomass is likely to be dependent on precipitation and temperature patterns (Branson 2008), May and June precipitation and average air temperature at a weather station $\sim30$ km from the site were similar between years.

Nitrogen content and vegetation quality typically decline with grass maturity (Heitschmidt et al. 1995, Oedekeken and Joern 2000) and with increasing grasshopper herbivory because of the removal of higher quality plant material (Redak and Capinera 1994; Branson 2003, 2006). However, nitrogen content of grass was higher with early season herbivory in 2004, when grass biomass was reduced by $\sim80\%$ (Fig. 2a and b). This likely resulted from grasshoppers removing a higher proportion of older graminoids, leading to younger warm season grasses and cool season grass regrowth comprising a higher percentage of the remaining biomass in cages with early season herbivory. Branson (2008) also found higher grass nitrogen content with higher levels of herbivory, when a large late summer rainfall event led to young plant material comprising a greater proportion of the total biomass with higher levels of herbivory.

Both the level of persistence of early season herbivory and the niche overlap between species should determine the importance of competitive effects among temporally separated herbivores (Chase and Belovsky 1994, Kaplan and Denno 2007, Behmer and Joern 2008). Because the both the number of individuals surviving and percent survival were lower with early season herbivory in 2004, prior herbivory lowered the carrying capacity for A. deorum nymphs. Although herbivory by nymph-overwintering grasshoppers could modify components of food quality other than nitrogen, exploitative competition from the reduction in grass biomass seems the most likely explanation for the decreased survival of A. deorum with prior herbivory in 2004. Because A. deorum nymphs and adults feed significantly on ground litter (Pfadt 2002), impacts of early season herbivory could be reduced for A. deorum.

Simultaneous high densities of nymph-overwintering and egg-overwintering species, as examined in this study, are likely to be an infrequent occurrence. No long-term population data exists at the study site, but the densities used in the experiment are within those observed in the northern Great Plains, especially if adjusted for bare ground that was avoided in cage placement. Foster et al. (2006) observed fall nymph-overwintering densities of $140/m^2$ in South Dakota, whereas Branson (2008) documented egg-overwintering densities of $\sim130/m^2$, where A. deorum was a major component of the grasshopper community. It is not possible to quantitatively assess how weather conditions and primary production during the period of the study compare with conditions associated with high grasshopper densities, because grasshopper population dynamics are determined by complex interacting biotic and climatic factors that operate over varying temporal scales (Branson et al. 2006). Furthermore, climate, soil, or vegetation patterns typically explain $<30\%$ of the variation in grasshopper densities at a site (Joern 2000).

Belovsky et al. (2000) hypothesized that herbivory from early emerging grasshopper species could reduce densities of later developing grasshoppers, but the results from this experiment indicate high levels of early season herbivory are needed to reduce nymphal survival of a later developing grasshopper. The results provide an indicator of the density range where competitive effects might be significant. Early season herbivory at a density of $16/m^2$ did not significantly reduce survival of A. deorum initiated at $40/m^2$, whereas early season herbivory at $60/m^2$ significantly reduced survival of A. deorum at $80$ individuals/m$^2$. Importantly, Belovsky et al. (2000) found an early hatching species reduced survival of a later developing species only when phenologies overlapped but not when placed in cages after the earlier hatching species died. Because early-instar A. deorum nymphs overlap with declining densities of adult nymph-overwintering grasshopper under field conditions, impacts of early season herbivory on nymphal A. deorum survival could be stronger than evident from this study. Early season herbivory could have additional effects if nymphal food limitation leads to delayed development and reduced reproduction of A. deorum (Danner and Joern 2004). Additional research is needed to fully address the importance of early season herbivory on population dynamics of abundant egg-overwintering grasshopper species.

Acknowledgments

D. Craig, J. Pacovsky, J. Anderson, K. Pfaff, S. Scott, E. Tiberi, and C. Vincent assisted with field and laboratory work.

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Received 31 December 2008; accepted 26 October 2009.