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Sean D. Whipple
University of Nebraska at Kearney

Mathew L. Brust
University of Nebraska-Lincoln, mbrust@csc.edu

Wyatt Hoback
University of Nebraska at Kearney, whoback@okstate.edu

Kerri M. Farnsworth-Hoback
University of Nebraska at Kearney, kefarns@okstate.edu

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Sean D. Whipple

Department of Biology
University of Nebraska at Kearney
905 West 25th Street
Kearney, NE 68849

Mathew L. Brust[1]

Department of Entomology
University of Nebraska–Lincoln
202 Plant Industry Building
Lincoln, NE 68583

W. Wyatt Hoback and **Kerri M. Farnsworth-Hoback**

Department of Biology
University of Nebraska at Kearney
905 West 25th Street
Kearney, NE 68849
hobackww@unk.edu

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ABSTRACT—A study of feeding preference was conducted on two tallgrass prairie grasshopper species, the autumn yellow-winged grasshopper *Arphia xanthoptera* (Burmeister) and the short-winged green grasshopper *Dichromorpha viridis* (Scudder), to determine if they would feed upon introduced grass species. Both grasshoppers were offered two non-native cool-season grasses, smooth brome (*Bromus inermis* Leyss) and Kentucky bluegrass (*Poa pratensis* L.), and two native warm-season grasses, big bluestem (*Adropogon gerardii* Vitman) and sideoats grama (*Bouteloua curtipendula* Michx.). Live biomass of the plants was weighed before and after feeding to quantify the amount of each plant species consumed by the grasshoppers. Statistical analysis showed that *D. viridis* strongly preferred smooth brome ($P \leq 0.05$) over other species offered. *A. xanthoptera* also consumed more smooth brome than the other grass species offered. These results suggest that both grasshopper species accept non-native grasses and perhaps prefer them to tallgrass prairie species. Because the tallgrass prairie ecosystem of the Great Plains has been dramatically impacted by human activity, documentation of the response of native insects to incursion by exotic plants is important to preservation efforts. Moreover, if grasshoppers feed on invasive sod-forming species such as smooth brome and Kentucky bluegrass, they may become an important ally in maintaining native plant diversity in remnant grassland ecosystems.

INTRODUCTION

The tallgrass prairie is a highly altered ecosystem of which less than 1% of the original prairie remains (Cully et al. 2003). Among impacts to this once vast ecosystem, human alterations include changes in land use, grazing regimes, fire regimes, and plant community composition (Samson and Knopf 1994). The intentional and accidental introductions of non-native species have further altered the ecosystem and increased pressures on the remaining prairie species. Among invertebrates shown to be impacted by changes to the tallgrass prairie ecosystem, much focus has been placed on butterflies, true bugs, and ground beetles (e.g., Arenz 1995; Swengel and Swengel, 1998). Less attention has focused on grasshoppers (Orthoptera: Acrididae)

[1]Current address: Department of Biology, Chadron State College, 1000 Main Street, Chadron, NE 69337

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because most species are generalist herbivores and thus (it is assumed), less likely to be impacted by changes to the plant community.

There are over 400 species of short-horned grasshoppers in the United States (Lockwood 2001), of which more than 100 occur in Nebraska (Brust et al. 2008). Short-horned grasshoppers (family Acrididae) are important because they are litter producers, valuable food for birds and other wildlife, and some species act as weed control agents on plants that are not palatable to livestock (Parker 1984). Some grasshoppers are also of significant economic importance as serious rangeland pests (Mulkern et al. 1969). Grasshopper species composition is largely determined by food plants and microhabitat characteristics (Joern and Lawlor 1981), and species may have narrow requirements for survival (Haarstad 1990; Ballard and Greenlee 1996; Reed 1996).

Most grasshoppers feed on a range of plants (Joern 1983) and as such are considered generalists with respect to diet breadth. However, grasshoppers are not indifferent feeders and often select plants with specific characteristics to gain required nutrients such as nitrogen (Behmer and Joern 1993). However, plants also contain physical and chemical defenses against herbivores. Specialist herbivores have evolved the ability to tolerate or overcome these defenses, which are effective in deterring generalists (species that consume a variety of food plants). Recent studies have shown that generalist grasshoppers respond to changes in plant species composition at the community level (Stoner and Joern 2004), and grasshopper herbivory may play a role in shaping the relative abundance of native and non-native plant species in invaded communities (Branson and Sword 2008). However, the response of native generalist insect herbivores such as grasshoppers to non-native plants has not often been quantified.

Smooth brome (*Bromus inermis* L.) is one of many non-native species that have become abundant in the Great Plains (Whitmore 2000) and remaining tallgrass prairie (Willson and Stubbendieck 1996). Kentucky bluegrass has been repeatedly introduced since the early 1800s and has become naturalized throughout much of the United States; it is listed as an invasive weed in the Great Plains states (Wenneberg 2004). Like other non-native grass species that occur in tallgrass prairies, smooth brome and Kentucky bluegrass are cool-season (C_3) plants (Cully et al. 2003). Their physiology and phenology is much different from the native prairie flora, which is dominated by warm-season (C_4) species. Smooth brome and Kentucky bluegrass grow actively during the fall and early spring, flowering in late spring or early summer; by midsummer, seed is mature (Howard 1996; Uchytil 1993). Kentucky bluegrass becomes nearly dormant during the midsummer while smooth brome will continue growing as long as moisture is available (Howard 1996; Uchytil 1993). Big bluestem does not begin actively growing in spring until several weeks after the cool-season grasses have begun green-up, flowering between July and September in Nebraska (Uchytil 1988). The timing of active growth and flowering of sideoats grama is very similar to that of big bluestem (Wasser 1982).

The incursion of smooth brome and other non-native cool-season plants in Nebraska is likely to have affected food availability for many tallgrass prairie herbivore species (Ogle et al. 2003). Porter and Redak (1997) demonstrated that *Melanoplus sanguinipes* Fabricius preferred native grasses over introduced grasses, although forbs comprised the largest proportion of their diet. Other prairie grasshopper species, including the autumn yellow-winged grasshopper *Arphia xanthoptera* (Burmeister) and the short-winged green grasshopper *Dichromorpha viridis* (Scudder), are also likely to have been impacted.

These two grasshopper species were chosen for study because little is known of their feeding preferences. Although *D. viridis* and *A. xanthoptera* occur throughout most of the eastern United States, both species are thought to be tallgrass prairie specialists (Bragg 1939; Wilbur and Fritz 1940; Reed 1996). We hypothesized that these species would prefer native warm-season grasses over non-native cool-season grasses. However, we found both grasshopper species to select non-native grasses in laboratory tests. Our results provide insight into response of native insect herbivores to non-native species and to the potential herbivore responses to non-native grass species on a dwindling tallgrass prairie ecosystem.

MATERIALS AND METHODS

Our methods were similar to those of Gangwere (1961), who observed grasshopper feeding damage on a range of test plants. However, we also collected quantitative data by weighing plant biomass before and after feeding trials. Adults of the green grasshopper and *A. xanthoptera* were collected from unmowed grassy areas using sweep nets at Lincoln Wilderness Park, Lancaster County, NE (4513667 N, 692758 E). Specimens were collected in late August of 2006 and 2007. After collection, grasshoppers were transported to the University of Nebraska at Kearney where each species was stored separately in plastic containers with plants from the collection site. Specimens were stored at room temperature (approximately 25°C) for two days prior to the feeding trials.

The day before each feeding trial was conducted, samples of four plant species were collected at Cottonmill Park and Recreation Area on the Oldfather Prairie Reserve, 2.4 km west of Kearney, NE. The four plant species chosen were smooth brome (*Bromus inermis* Leyss.), big bluestem (*Adropogon gerardii* Vitman), sideoats grama (*Bouteloua curtipendula* Michx.), and Kentucky bluegrass (*Poa pratensis* L.). Specimens of the four plant species were selected based on healthy appearance (green, unwilted). Samples were collected from multiple plants (5 to 10 depending on species) by snipping the base of plants using garden shears and wrapping vegetation in a moist paper towel. After collection, the plants were placed in water overnight to prevent dehydration.

Feeding studies consisted of placing a single grasshopper specimen into a container with each of the four plant species. Prior to feeding studies, sections approximately 25 cm long from the tip of the stem were prepared. In 2006 each plant specimen was examined for damage, weighed to the nearest hundredth of a gram, and placed into a small cylindrical tube. The sections of grasses weighed approximately 0.8 g for sideoats grama, 1.3 g for the big bluestem and Kentucky bluegrass, and 3.0 g for smooth brome. The tubes were filled with a water-saturated cotton ball to keep the plants from drying out during the feeding trial. A steel ball was also placed in the bottom of the tubes to prevent them from falling over from the weight of the plant or the grasshoppers feeding on them. Ten replicates were created for each grasshopper species, for a total of 20 containers with four plant species per container. The containers were then placed into a growth chamber at 25°C on a 12:12 light/dark cycle. The containers were left in the growth chamber for three days to allow for feeding, and then removed to weigh the plants. Each plant was examined for damage to leaves from feeding. All remaining material was weighed to the nearest hundredth of a gram. Any clippings that had fallen to the bottom of the container were identified by texture and appearance and were weighed and included in the totals of mass remaining after feeding.

The experiment was repeated in 2007 with 15 replicates per grasshopper species. As a control for mass change associated with water uptake, six containers were prepared in the same manner as the experimental groups, except that no grasshopper was put in with the plants. Plants were weighed before placing them in the growth chamber and after three days. Gains in mass were interpreted as water uptake by the plant.

Feeding preference data were analyzed following the methods Rodrigues et al. (2008). Once data were collected, a nonparametric Kruskal-Wallis one-way analysis of variance was performed to analyze feeding on the four plant species by each grasshopper species and by each year. If significant differences were detected among the groups, Dunn's method of pairwise comparisons was used to separate the means.

RESULTS

The control showed that no plants suffered mass loss after three days in the growth chamber. Mean water uptake for smooth brome was 0.075 g. Sideoats grama and Kentucky bluegrass also gained mass from water uptake (0.068 g and 0.093 g, respectively). Big bluestem had a slightly higher mean level of water uptake at 0.151 g. Total mass gain was between 3% and 16% across plant species. These values were not significantly different across the four plant species ($P = 0.469$).

In 2006 the 10 *A. xanthoptera* consumed a total of 1.18 g of smooth brome compared to 0.10 g of sideoats grama, 0.22 g of big bluestem, and 0.13 g of Kentucky bluegrass (Fig. 1). Feeding was evident on all the samples of smooth brome, while in many cases the other three species of plant were not fed upon. Grasshoppers ate significantly more smooth brome ($P \leq 0.05$) than sideoats grama or Kentucky bluegrass. Although grasshoppers ate more brome grass than big bluestem (Fig. 1), the difference was not significant ($P = 0.076$). Individual grasshoppers ate variable amounts of grasses with one *A. xanthoptera* consuming 0.54 g of smooth brome.

In 2007 the 15 *A. xanthoptera* together consumed a total of 7.53 g, with smooth brome comprising 64% (4.82 g) of the total. Kentucky bluegrass, the other non-native grass, accounted for 2.31 g of the total, while sideoats grama and big bluestem accounted for 0.21 and 0.20 g, respectively (Fig. 1). Mean consumption of smooth brome was 0.321 g per grasshopper with two of the grasshoppers tested exhibiting no feeding on smooth brome. *A. xanthoptera* showed much less feeding on the other plant species, with a mean consumption of 0.014 g of sideoats grama, 0.013 g of big bluestem, and 0.157 g of Kentucky bluegrass. In 2007 grasshoppers consumed significantly more smooth brome ($P \leq 0.001$) than other plant species, with the exception of Kentucky bluegrass ($P = 0.280.05$) (Fig. 1), although there was variation among individuals.

D. viridis strongly preferred smooth brome in both years. In 2006 individuals consumed a total of 2.38 g of smooth brome, compared to 0.37 g of sideoats grama, 0.30 g of big

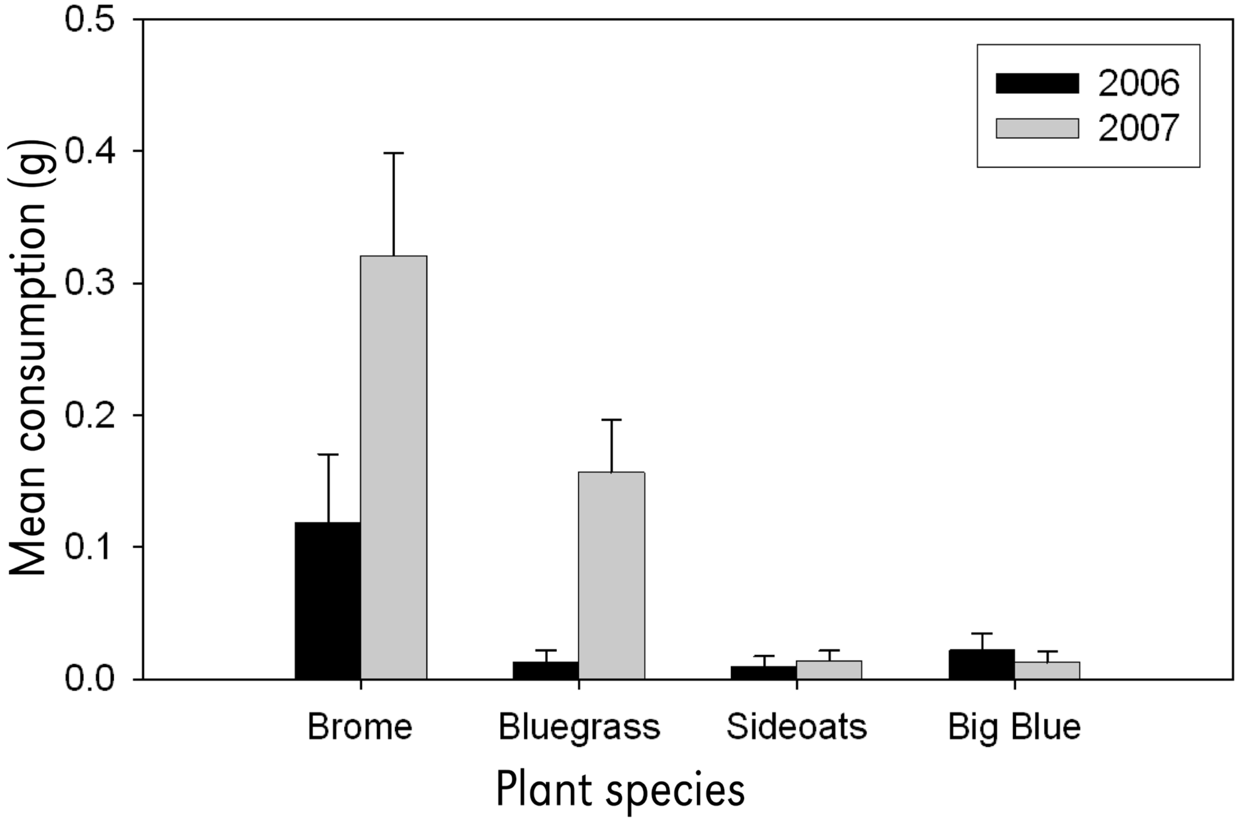

Figure 1. The mean amount (±1 standard error) of each plant species consumed by the autumn yellow-winged grasshopper, *Arphia xanthoptera*, in laboratory feeding trials in 2006 (N = 10) and 2007 (N = 15). Brome = smooth brome (*Bromis inermis*) and Bluegrass = Kentucky bluegrass (*Poa pratensis*) are non-native cool-season species); Sideoats = sideoats grama (*Bouteloua curtipendula*) and Big Blue = big bluestem (*Adropogon gerardii*) are native warm-season grasses.

bluestem, and 0.13 g of Kentucky bluegrass, with feeding evident on all samples of smooth brome (Fig. 2). In all cases, *D. viridis* were feeding on brome when the container was opened to weigh the plants at the end of the trial. Although there was more evidence of feeding on the other three plant species than was observed for *A. xanthoptera*, consumption of smooth brome was significantly higher than that of the three other plant species ($P \leq 0.001$; Fig. 2).

In 2007 *D. viridis* ate a total of 5.89 g of all plants, with smooth brome representing 83% (4.88 grams) of the total plant mass consumed, significantly more ($P < 0.001$) than the other tested species (Fig. 2). Kentucky bluegrass consumption was second highest with a total of 0.63 g. Sideoats grama and big bluestem consumption totaled 0.22 g and 0.17 g, respectively. Smooth brome was the only plant species to show evidence of feeding by all individual grasshoppers.

The number of plant species consumed by each individual grasshopper was also compared (Table 1). Both species of grasshopper fed on two plant species in most of the trials. *A. xanthoptera* consumed one, two, or three plants, but never consumed all four. *D. viridis* sampled all plants in 28% of trials.

TABLE 1

PERCENTAGE OF TOTAL NUMBER OF GRASSHOPPERS OF EACH SPECIES (N = 25) FEEDING ON ONE OR MORE OF THE OFFERED PLANT SPECIES

	Number of plant species fed upon			
Grasshopper species	**1**	**2**	**3**	**4**
Arphia xanthoptera	20%	44%	36%	0%
Dichromorpha viridis	20%	36%	16%	28%

DISCUSSION

Our experiments revealed surprising results: Two grasshopper species hypothesized to be tallgrass prairie specialists fed preferentially on non-native smooth brome and Kentucky bluegrass over grasses readily available

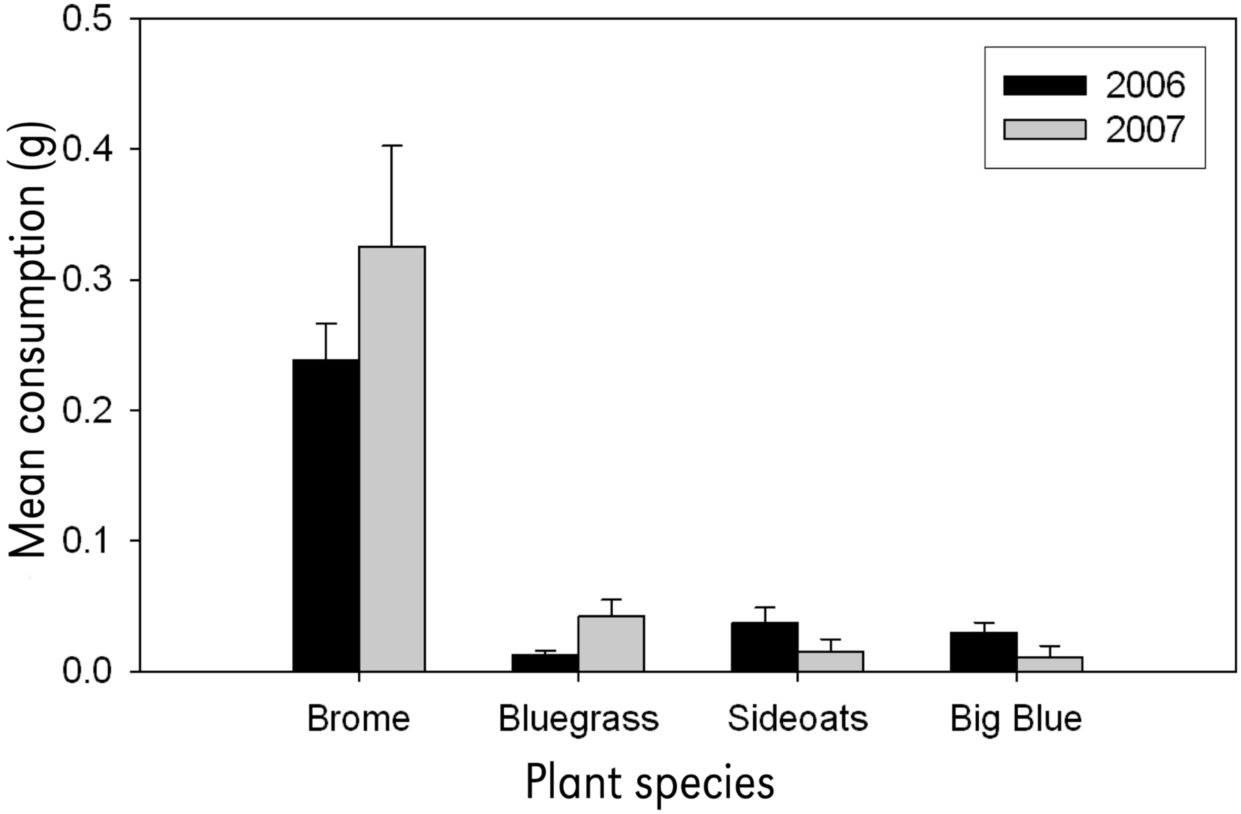

Figure 2. The mean amount (±1 standard error) of each plant species consumed by short-winged green grasshopper, *Dichromorpha viridis*, in laboratory feeding trials in 2006 ($N = 10$) and 2007 ($N = 15$). Brome = smooth brome (*Bromis inermis*) and Bluegrass = Kentucky bluegrass (*Poa pratensis*) are non-native cool-season species); Sideoats = sideoats grama (*Bouteloua curtipendula*) and Big Blue = big bluestem (*Adropogon gerardii*) are native warm-season grasses.

in native tallgrass prairie. Both *A. xanthoptera* and *D. viridis* consumed more smooth brome than other grass species offered. This observation can either be attributed to the grasshoppers encountering a relatively novel food or having shifted their diet choices because of the abundance of smooth brome within their community. In our experiments, we tested non-native cool-season grasses versus warm-season grasses commonly found in native tallgrass prairies. Because these grasses are very different phylogenetically and physiologically, the latter explanation seems most likely. For *A. xanthoptera*, analysis of the 2006 trials showed a statistical difference between smooth brome and all other plants tested, except the native big bluestem. In 2007 smooth brome consumption was significantly higher than all plants except Kentucky bluegrass. While we cannot know whether *A. xanthoptera* historically fed upon native cool-season grasses, our results suggest that cool-season non-native grasses are acceptable and even preferred food plants during the late summer.

D. viridis are adults in summer and fall, and eggs hatch in the spring (Otte 1981). *A. xanthoptera* adults are present July through November (Otte 1984). Time of hatching and maturation may be related to preference for cool-season versus warm-season grasses. If smooth brome is readily available and contains the necessary nutrients for survival and reproduction, it is not surprising that it is utilized (Ueckert et al. 1972). However, because of defense compounds, it is rare for even generalist herbivores to eat non-native species, especially when native species are present (Hierro and Callaway 2003; Zhang and Jiang 2006). Hinks and Olfert (1999) previously showed nymphal *Melanoplus sanguinipes* to survive on smooth brome. However, Olfert et al. (1994) found that of the plants tested, smooth brome was the most detrimental and resulted in slower development and a lower mean dry weight.

The difference in results may also be a result of different plant nutrient levels, as Joern and Behmer (1997) demonstrated for *Ageneotettix deorum*. It is difficult to predict whether the feeding preferences of grasshoppers tested in this study would be different if tested earlier in the season or when they are in the nymphal stage. Future studies should examine feeding preferences of more grasshopper species with more plant choices to separate phenology, plant physiology, and nutrient condition.

Various authors have debated whether generalist insect herbivores prefer cool-season or warm-season plant species (e.g., Boutton et al. 1978; Pinder and Kroh 1987). Heidorn and Joern (1984) found that *Ageneotettix deorum* (Scudder), preferred cool-season grasses over warm-season grasses. They found no correlation between preference and leaf water content, crude protein content, or toughness. They concluded that differences in leaf anatomy between cool-season and warm-season grasses resulted in the observed preference. Our results lend only partial support to this assertion. While the food plant chosen by both grasshopper species was a cool-season grass, the two cool-season species were not always clearly preferred over the warm-season grasses offered. For some individuals, the amount of Kentucky bluegrass consumed was lower than the amount eaten of either species of warm-season grass. Although we tested different species of grasses and grasshoppers, Heidorn and Joern's conclusion that leaf anatomy is a strong influence on grasshopper feeding preference for cool-season grasses appears to be invalid.

Behmer and Joern (1993) demonstrated that grasshoppers feed based on a need for a limiting nutrient. During development, grasshoppers are often limited by nitrogen, which they use for molting, growth, and reproduction (Joern and Behmer 1997). Because these grasshoppers are adults late in the season, plants in our study were collected in late August. The warm-season grasses had already flowered and Kentucky bluegrass may have been dormant. It is possible that smooth brome was preferred because it was the only actively growing food plant. However, the relationship between food preference and leaf water content has been studied by others, with conflicting results. Some studies resulted in little or no correlation between leaf water content and feeding preference (Gangwere 1961; Heidorn and Joern 1984). Lewis (1984) showed that *Melanoplus differentialis* Thomas prefers to feed on the wilted vegetation of the wild sunflower, *Helianthus annuus* L., rather than undamaged tissue. If grasshoppers prefer water-stressed plants, then we would expect that the plants that took up the most water in our study to also be those that were preferred. Because mean water uptake was not significantly different among the plants we tested, we cannot resolve this question.

It is difficult to draw conclusions about feeding choices from the percentage of individual grasshoppers that consumed a single versus several plant species. In some trials, a single plant was fed upon, and in others, all plants were sampled. Grasshoppers have been shown to feed on one plant during preference studies and then, on the following day, show a significantly different preference (Behmer and Joern 1993; Howard 1993). In addition, grasshoppers are known to sample many plant species prior to feeding upon a single species (Haldar et al. 1995). In our experiments, none of the *A. xanthoptera* individuals consumed all four plant species, nor did they all avoid the same plant. The fact that 28% of *D. viridis* fed on all four plants offered suggests that they are either more generalist feeders or that they sample many potential food plants prior to feeding.

Smooth brome and Kentucky bluegrass are sod-forming grasses. These species have the capacity to form near-monocultures and thus may be more "apparent" to herbivores than more sparsely or patchily distributed species, such as big bluestem and sideoats grama, which are both bunchgrasses. Because plants that are more apparent have a higher probability of insect attack, they are more likely to employ constitutive (rather than induced) defenses (Zangerl and Rutledge 1996). We would also expect the non-native grasses we tested to be more heavily defended than the native bunchgrasses tested. Defenses against herbivory can allow some invasive plant species to outcompete native plants, displacing them. Such a phenomenon is often explained in terms of "the enemy release hypothesis," which predicts exotic plants to become invasive when they leave behind specialist herbivores from their native range and are successful in deterring generalist herbivores in their new range (Keane and Crawley 2002). In their study of feeding by two native generalist grasshoppers on various invasive and noninvasive plant species, Jogesh et al. (2008) found a negative correlation between feeding and level of plant invasiveness in one species of grasshopper but not the other. While we did not directly study defensive compounds, our results suggest that the autumn and green grasshopper are not deterred from feeding on smooth brome and Kentucky bluegrass, despite the expectation that these two species would be well-defended against herbivory.

Grasshoppers can exert a strong effect on plant community composition. Branson and Sword (2008) found that grasshopper herbivory reduced native plant species richness and abundance in a community dominated by crested wheatgrass. We found that the two tested species preferred non-native cool-season grasses over native grasses. Potentially, these insect species can aid in maintaining plant diversity in remnant prairies (Porter and Redak 1997) by differentially feeding upon invasive grasses. Identifying the roles grasshoppers may play in conserving native prairie should become a research priority. The impacts of grasshopper herbivory on plants that decrease or increase under heavy grazing should also be investigated to better understand the interplay between invertebrate herbivores and grazing livestock in determining plant community characteristics. Further study to identify feeding preferences for individual grasshopper species would provide insights into these ecological interactions and guide management decisions that impact both plants and grasshoppers.

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REFERENCES

Arenz, C.L. 1995. Initiation of a butterfly monitoring program at the Tallgrass Prairie Preserve, Osage County, Oklahoma. *Proceedings of the Oklahoma Academy of Sciences* 75:25-29.

Ballard, H.E., Jr., and E.S. Greenlee. 1996. *Field surveys for potentially rare Missouri Orthoptera*. Report to the Missouri Department of Conservation, Columbia, MO.

Behmer, S.T., and A. Joern. 1993. Diet choice by a grass-feeding grasshopper based on the need for a limiting nutrient. *Functional Entomology* 7:522-27.

Boutton, T.W., G.N. Cameron, and B.B. Smith. 1978. Insect herbivory on C_3 and C_4 grasses. *Oecologia* 36:21-32.

Bragg, J.H. 1939. The geographic distribution of Acrididae in northern Oklahoma. *American Midland Naturalist* 22:660-75.

Branson, D.H., and G.A. Sword. 2008. Grasshopper herbivory affects native plant diversity and abundance in a grassland dominated by the exotic grass *Agropyron cristatum*. *Restoration Ecology* 17:89-96.

Brust, M.L., W.W. Hoback, and R.J. Wright. 2008. A synopsis of Nebraska grasshopper distributions. *Journal of the Kansas Entomological Society* 81:208-55.

Cully, A.C., J.F. Cully Jr., and R.D. Hiebert. 2003. Invasion of exotic plant species in tallgrass prairie fragments. *Conservation Biology* 17:990-98.

Gangwere, S.K. 1961. A monograph on food selection in Orthoptera. *Transactions of the American Entomological Society* 87:67-230.

Haldar, P., K.P. Bhandar, and S. Nath. 1995. Observations on food preferences of an Indian grasshopper *Acrida exaltata* (Walker) (Orthoptera: Acrididae: Acridinae). *Journal of Orthoptera Research* 4:57-59.

Haarstad, J. 1990. *The Acrididae of Minnesota*. Minnesota Department of Natural Resources Final Report, St. Paul, MN.

Heidorn, T., and A. Joern. 1984. Differential herbivory on C_3 versus C_4 grasses by the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia* 65:19-25.

Hierro J.L., and R.M. Callaway. 2003. Allelopathy and exotic plant invasion. *Plant and Soil* 256:29-39.

Hinks, C.F., and O. Olfert. 1999. Growth and survival of early-instar grasshoppers on selected perennial grasses, with observations on plant constituents which may influence performance. *Journal of Orthoptera Research* 8:237-42.

Howard, J.J. 1993. Temporal pattern of resource use and variation in diets of individual grasshoppers (Orthoptera: Acrididae). *Journal of Insect Behavior* 6:441-53.

Howard, J.L. 1996. *Bromus inermis*. In *Fire Effects Information System* (online). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/ (accessed February 19, 2009).

Joern, A. 1983. Host plant utilization by grasshoppers (Orthoptera: Acrididae) from a Sandhills prairie. *Journal of Range Management* 36:793-97.

Joern, A., and S.T. Behmer. 1997. Importance of dietary nitrogen and carbohydrates to survival, growth, and reproduction in adults of the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia* 112:201-8.

Joern, A., and L.R. Lawlor. 1981. Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos* 37:93-104.

Jogesh, T., D. Carpenter, and N. Cappuccino. 2008. Herbivory on invasive exotic plants and their noninvasive relatives. *Biological Invasions* 10:797-804

Keane, R.M., and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17:164-70.

Lewis, A.C. 1984. Plant quality and grasshopper feeding: Effects of sunflower condition on preference and performance in *Melanoplus differentialis*. *Ecology* 65:836-43.

Lockwood, J.A. 2001. Voices from the past: What we can learn from the Rocky Mountain locust. *American Entomologist* 47:208-15.

Mulkern, G.B., K.P. Pruess, H. Knutson, A.F. Hagen, J.B. Campbell, and J.D. Lambley. 1969. *Food habits and preferences of grassland grasshoppers of the north central Great Plains*. North Dakota Agricultural Experiment Field Station, North Central Regional Publication no. 481.

Ogle, S.M., W.A. Reiners, and K.G. Gerow. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* 149:46-58.

Olfert, O., C.F. Hinks, R.M. Weiss, and S.B.M. Wright. 1994. The effect of perennial grasses on growth, development and survival of grasshopper nymphs (Orthoptera: Acrididae): Implications for population management in roadsides. *Journal of Orthoptera Research* 2:1-3.

Otte, D. 1981. *The North American Grasshoppers*, vol. 1, *Acrididae: Gomphocerinae and Acridinae*. Harvard University Press, Cambridge, MA.

Otte, D. 1984. *The North American Grasshoppers*, vol. 2: *Acrididae: Oedipodinae*. Harvard University Press, Cambridge, MA.

Parker, M. 1984. Local food depletion and the foraging behavior of a specialist grasshopper, *Hesperotettix viridis*. *Ecology* 65:824-35.

Pinder, J.E., III, and G.C. Kroh. 1987. Insect herbivory and photosynthetic pathways in old-field ecosystems. *Ecology* 68:254-59.

Porter, E.E., and R.A. Redak. 1997. Diet of migratory grasshopper (Orthoptera: Acrididae) in a California native grassland and the effect of prescribed spring burning. *Environmental Entomology* 26:234-40.

Reed, C. 1996. List of insect species which may be tallgrass prairie specialists. In *Final Report to the USFWS Cooperating Agencies, Conservation Biology Research Grants Program, Division of Ecological Services*. Minnesota Department of Natural Resources, St. Paul, MN.

Rodriques, D., G.L.G. Soares, and G.R.P. Moreira. 2008. Feeding preference of *Holymenia clavigera* and *Anisoscelis foliacea marginella* (Hemiptera: Coreidae: Anisoscelini) in relation to intra- and interspecific features of host plants (Passifloraceae). *Environmental Entomology* 37:1323-31.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418-21.

Stoner, K.L. and A. Joern. 2004. Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecological Applications* 14:1306-20.

Swengel, A.B., and S.R. Swengel. 1998. Tall-grass prairie butterflies and birds. In *Status and Trends of the Nation's Biological Resources*, ed. M.J. Mac, P.A. Opler, C.E. Puckett Haecker, and P.D. Doran, 2:446-47. U.S. Department of the Interior, U.S. Geological Survey, Washington, DC.

Uchytil, R.J. 1988. *Andropogon gerardii* var. *gerardii*. In *Fire Effects Information System* (online). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/ (accessed February 19, 2009).

Uchytil, R.J. 1993. *Poa pratensis*. In *Fire Effects Information System* (online), U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, http://www.fs.fed.us/database/feis/ (accessed February 19, 2009).

Ueckert, D.N., R.M. Hansen, and C. Terwilliger, Jr. 1972. Influence of plant frequency and certain morphological variations on diets of rangeland grasshoppers. *Journal of Range Management* 25:61-65.

Wasser, C.H. 1982. Ecology and culture of selected species useful in revegetating disturbed lands in the West. FWS/OBS-82/56. U.S. Department of the Interior, Fish and Wildlife Service, Office of Biological Services, Western Energy and Land Use Team, Washington, DC.

Wenneberg, S. 2004. Kentucky bluegrass, *Poa praetensis* L. *USDA NRCS Plant Guide* (online). U.S. Agricultural Society Natural Resources Conservation Service. http://plants.usda.gov/plantguide/pdf/pg_popr.pdf (accessed June 8, 2009).

Whitmore, J.S. 2000. Forage grasses for drought-prone areas. In *Drought Management on Farmland*, ed. V.P. Singh, 35:252-75. Kluwer Academic Publishers, Norwell, MA.

Wilbur, D.A., and R.F. Fritz. 1940. Grasshopper populations (Orthoptera: Acrididae) of typical pastures in the bluestem region of Kansas. *Journal of the Kansas Entomological Society* 13:86-100.

Willson, G.D., and J. Stubbendieck. 1996. Suppression of smooth brome by atrazine, mowing, and fire. *Prairie Naturalist* 28:13-20.

Zangerl, A.R., and C.E. Rutledge. 1996. The probability of attack and patterns of constitutive and induced defense: A test of optimal defense theory. *American Naturalist* 147:599-608.

Zhang, D., and X. Jiang. 2006. Interactive effects of habitat productivity and herbivore pressure on the evolution of anti-herbivore defense in invasive plant populations. *Journal of Theoretical Biology* 242:935-40.