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GRASSHOPPER DIETARY (ORTHOPTERA: ACRIDIDAE) FROM A NEBRASKA SAND HILLS PRAIRIE

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Species-specific selection of host plants by grasshoppers from a Sand Hills grassland in Nebraska is documented by identifying fragments of plants from the foregut. Results from this study are compared with a similar study performed in a mixed-grass pasture near North Platte, Nebraska. On average, a larger number of plants was included in the diet of species at Arapaho Prairie. Differences in specific composition of diets were observed in some cases.

† † †

INTRODUCTION

Patterns of herbivory for insects vary greatly (Brues, 1946; Cates, 1980; Futuyma, 1983; Otte and Joern, 1977). Although there are notable exceptions, differences exist among major taxa in reasonably predictable ways. For example, temperate species of Lepidoptera tend to be specialized feeders while grasshoppers (Orthoptera: Acrididae) are more polyphagous (Futuyma, 1976; Joern, 1979). However, even within groups of herbivorous insects, such as the Acrididae, use of a wide range of host plants is evident (Gangwere, 1961; Joern, 1979 and 1983; Mulkern, 1967; Mulkern et al., 1969; Otte and Joern, 1977; Pfadt and Lavigne, 1982; Sheldon and Rogers, 1978; Ueckert and Hansen, 1971). Understanding mechanisms underlying such patterns has been greatly aided by examining diets of coexisting grasshopper species from a variety of habitats. Results presented here add to the increasing number of studies that are beginning to produce a pattern that is adequate to spawn more intensive research on the causes underlying selection of host plants by grasshoppers. Grasshopper diets from a Nebraska Sand Hills prairie are presented and compared with similar studies from other grassland habitats.

STUDY SITE

Arapaho Prairie is typical upland Sand Hills grassland located in Arthur County, Nebraska (southwestern portion of the Sand Hills). Extensive sand dunes are the dominant topographic feature of this site. Vegetational communities have been described in detail (Barnes, 1980; Keeler et al., 1980); approximately 200 species of plants from 45 families (including some aquatic taxa) have been recorded.

Forty-two species of grasshoppers have been collected from Arapaho Prairie in various degrees of abundance and phenological patterns (Joern, 1982). Species included in the analysis of diet represent more common species which are typically adults in July through September. Detailed descriptions of the patterns of abundance are contained in Joern (1982).

METHODS

Species-specific diets of grasshoppers were determined by examining gut contents under a compound microscope at 100x power (Mulkern et al., 1969; Joern, 1979; Otte and Joern, 1977). Adult grasshoppers were killed immediately after capture and the foreguts removed and stored in 70% ethanol within 1 hr after death. Fragments of plants in the gut were compared with permanently mounted reference slides of plants from the study site. Entire slides were scanned and plants were identified on the basis of structure of cell walls, patterns of stomata, and trichomes. Most fragments could be identified to species although some did not have recognizable characters suitable for species-level identification; these are

lumped as *unknown* grasses or forbs. Other fragments had unique characters that could not be matched with samples from the study site. These fragments were coded as unique but otherwise *unidentified* taxa. All fragments of insects were lumped.

Abundances of plants in the gut were weighted as follows. The most abundant material in the gut was scored as such, and all other plant species were recorded as present. These data were weighted to give species-specific dietaries. Food plants that were most abundant in the gut were weighted three times as much as food plants recorded as present in each gut. Composite diets of individual species were then calculated. The most abundant plant was nearly always unambiguously obvious as it easily dominated the composition of a particular sample.

An index of diet breadth (B) is calculated based on an index that weights the proportion (p_i) of each food plant taken:

$$B = \exp(H')$$

where

$$H' = - \sum_i p_i \ln p_i$$

RESULTS AND DISCUSSION

Diets at Arapaho Prairie

Species-specific diets are shown in Table I. Clearly, a wide range of food plants is included in the diets of these species. Overall, 77 food categories (excluding unknown grasses, forbs, or flower parts) were used. Based on collecting records (Keeler et al., 1980), this represents 43% (76/179) of the dry prairie species recorded at Arapaho Prairie. Forbs constituted 37.3%, grasses and sedges 58%, and insects 4.8% of the composite diet; relative abundances of grasshopper species were not accounted for in these calculations. Forbs make up about 22% of the available vegetation while grasses and sedges contribute the remainder (78%) at Arapaho Prairie (Barnes, 1980).

Although a wide range of food plants is taken by the collective grasshopper assembly at Arapaho Prairie, species are not indiscriminate feeders. Clear subfamily distinctions are evident as gomphocerines and oedipodines are primarily grass-feeders and melanoplinae forb-feeders. Also, the overall pattern of food plant use by grasshoppers in western Texas differed significantly from a pattern expected if use of host plants were random (Joern and Lawlor, 1980). I have obtained similar results for the grasshopper species from Arapaho Prairie.

A distribution of diet breadths is shown in Figure 1. Many kinds of grasshoppers feed on a wide variety of host plants.

Interestingly, the majority of species with small diet breadths are grass-feeders and gomphocerines, while the majority of the species with large diet breadths are forb-feeders and
(continued on page 31)

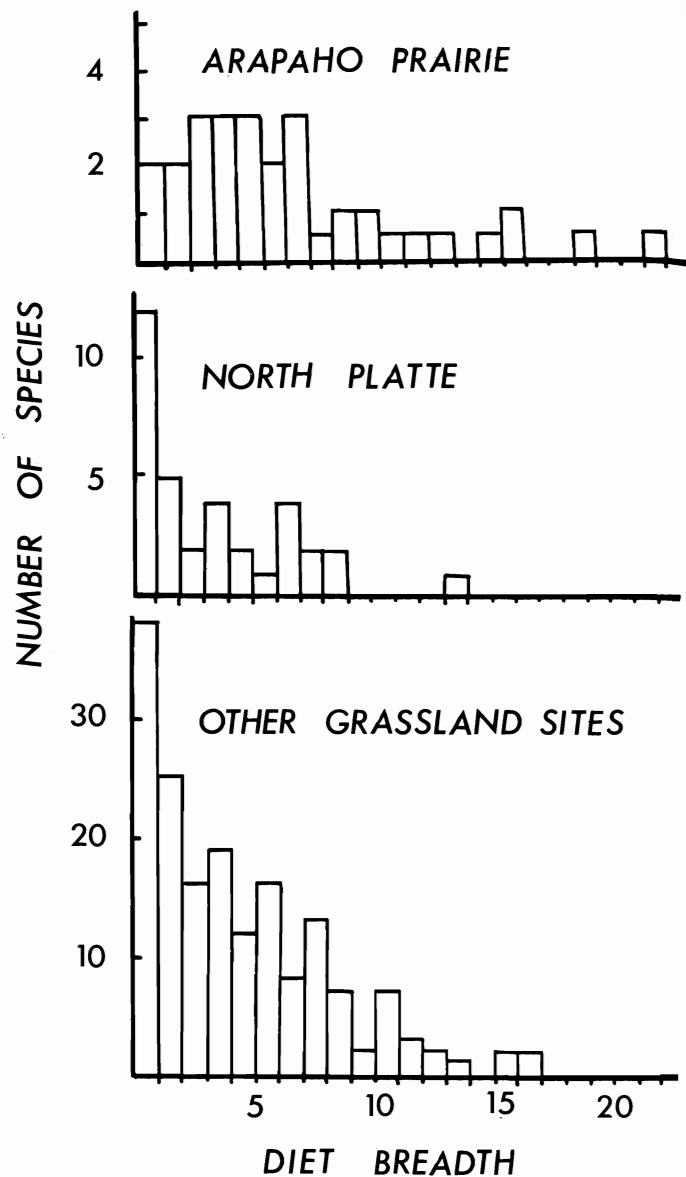


FIGURE 1. Distributions of grasshopper diet breadth at Arapaho Prairie (this study), North Platte, Nebraska (Mulkern et al., 1969), and a composite of other available grassland studies. Species included in other grassland studies are those from western Texas arid grasslands (Joern, 1979), northern United States grasslands (Mulkern et al., 1969), Colorado sandhills rangeland (Ueckert and Hansen, 1971), and Colorado short-grass prairie (Pfadt and Lavigne, 1982). Values of diet breadth that are integers are included in the next category (e.g., both 1.0 and 1.7 are included in the category between 1 and 2).

TABLE I. Diets of grasshopper species from a Sand Hills prairie in Nebraska (USA). Use of a particular plant species is presented as a proportion in which the plant species is used by the grasshopper species relative to all other plant species in the grasshopper's diet (after weighting abundance in individual guts). Only plant species found in the collective diet are presented. An asterisk (*) indicates that the food plant constitutes less than 1% of the diet of a particular grasshopper species. Relative abundance (top of table) represents the proportion of a particular plant species in the environment relative to all other plant species present at the site (after Barnes, 1980); an asterisk indicates that the relative abundance is less than 1%. Relative use is the proportion that a particular plant species is found in the overall collective diet of all grasshopper species (weighted equally). Letter identifications represent unique plant taxa which could not be matched to known taxa at the site and given a name. Unknown categories did not have unique characters. Plant families are coded: 1. Cyperaceae, 2. Poaceae, 3. Amaranthaceae, 4. Asteraceae, 5. Boraginaceae, 6. Brassicaceae, 7. Chenopodiaceae, 8. Fabaceae, 9. Loaceae, 10. Malvaceae, 11. Onagraceae, 12. Plantaginaceae, and 13. Solanaceae.

	<i>Carex heliophila</i> Mack.	<i>C. praegracilis</i> Bailey	<i>Agropyron smithii</i> Rydb.	<i>Andropogon hallii</i> Hack.	<i>A. scoparius</i> Michx.	<i>Bouteloua gracilis</i> (H.B.K.) Griffiths	<i>B. hirsuta</i> Lag.	<i>Calamovilfa longifolia</i> (Hook.) Scribn.	<i>Festuca octaflora</i> Walt.	<i>Koeleria pyramidata</i> (Lam.) Beauv.
Plant Family	1	1	2	2	2	2	2	2	2	2
Relative Abundance	5.6	*	1.6	6.5	3.8	21.5	10.8	21.1	*	7.3
Grasshopper Species	Sample Size									
Gomphocerinae										
<i>Acrolophitus hirtipes</i>	50									
<i>Ageneotettix deorum</i>	74	*	0.13			0.40	0.18	0.12		0.03
<i>Amphitornus coloradus</i>	49	*	0.04			0.87	0.02	0.04		0.07
<i>Cordillacris occipitalis</i>	51		0.14	0.03	0.08	0.39	0.06	0.13		
<i>Eritettix simplex</i>	20	0.37		0.05		0.16		0.32		0.05
<i>Mermiria bivittata</i>	60	0.03	0.13	0.03	0.15	0.15		0.32		
<i>Opeia obscura</i>	50				0.08	0.75	0.05	0.04		
<i>Parapomala wyomingensis</i>	50	*	*	0.20	0.15	0.05	0.07	0.39		
<i>Phlibostroma quadrimaculatum</i>	50				0.07	0.66	0.09	0.08		0.04
<i>Psoloessa delicatula</i>	84	0.25	0.08	0.02		0.44	0.05	0.03		0.06
Oedipodinae										
<i>Arphia conspersa</i>	28	0.68			0.03	0.05		0.05		0.04
<i>A. pseudonietana</i>	49		0.14		*	0.12	0.03	0.08		0.14
<i>Dissosteira carolina</i>	18		0.11	0.09	0.11	0.07		0.07		
<i>Hippiscus ocelote</i>	16	0.03	0.05	0.02	0.05	0.17	0.47	0.03		
<i>Spharagemon collare</i>	50	0.01	0.02	0.09	0.04	0.07	0.05	0.25	0.01	0.01
<i>Trachyrhachys kiowa</i>	50		0.03		0.01	0.80	0.02			0.14
<i>Trimerotropis citrina</i>	15	0.11			0.04			0.06		
Melanoplinae										
<i>Aeoloplides turnbulli</i>	51									
<i>Hesperotettix speciosus</i>	44							0.01		
<i>H. viridis</i>	50					*				
<i>Hypochlora alba</i>	49									
<i>Melanoplus angustipennis</i>	50	0.12	0.01		0.02	0.06	0.03	0.01		
<i>M. bivittatus</i>	51			0.05		0.07	*	0.07		
<i>M. confusus</i>	43				0.04	0.01	*	0.03		
<i>M. differentialis</i>	50	0.02	0.21	0.23		*				
<i>M. femurrubrum</i>	19					0.01				
<i>M. flavidus</i>	50	*			*	*	*			
<i>M. foedus</i>	46	*			0.02	0.07	0.01	*		
<i>M. gladstoni</i>	40	0.07	*		0.01	0.12	0.03	*		
<i>M. sanguinipes</i>	50	0.06	0.07	0.01		0.15	0.04	0.03		0.02
<i>Phoetaliotes nebrascensis</i>	52	0.18	0.11	0.05	0.14	0.10	0.02	0.06		0.02
Relative Use	0.07	0.01	0.05	0.02	0.04	0.20	0.04	0.08	*	0.02

TABLE I (Continued).

	<i>Muhlenbergia pungens</i> Thurb.	<i>Panicum oligosanthes</i> Schult, var. <i>scribnerianum</i> (Nash.) Fern.	<i>P. virgatum</i> L.	<i>Paspalum setaceum</i> Michx.	<i>Sorghastrum avenaceum</i> (Michx.) Nash.	<i>Stipa comata</i> Trin. and Rupr.	<i>Sporobolus cryptandrus</i> (Torr.)	<i>Amaranthus</i> sp.	<i>Froelichia floridana</i> (Nutt.) Mag.	<i>Ambrosia artemisiifolia</i> L.
Plant Family	2	2	2	2	2	2	2	3	3	4
Relative Abundance	*	*	6.0	*	*	11.7	*	*	*	*
Grasshopper Species										
Gomphocerinae										
<i>Acrolophitus hirtipes</i>										
<i>Ageneotettix deorum</i>						0.02				
<i>Amphitornus coloradus</i>						0.03				
<i>Cordillacris occipitalis</i>						0.10				
<i>Eritettix simplex</i>										
<i>Mermiria bivittata</i>			0.02		0.02	0.05				
<i>Opeia obscura</i>					0.03	0.05				
<i>Parapomala wyomingensis</i>					0.02	0.04				
<i>Phlibostroma quadrimaculatum</i>					0.02	0.03				
<i>Psoloessa delicatula</i>										
Oedipodinae										
<i>Arphia conspersa</i>										
<i>A. pseudonietana</i>	0.02				0.03	0.14				
<i>Dissosteira carolina</i>		0.04	0.04							
<i>Hippiscus ocelote</i>			0.02				0.05			
<i>Spharagemon collare</i>										
<i>Trachyrhachys kiowa</i>						0.05				
<i>Trimerotropis citrina</i>	0.01									
Melanoplinae										
<i>Aeoloplides turnbulli</i>										
<i>Hesperotettix speciosus</i>								0.02		0.09
<i>H. viridis</i>				0.02						
<i>Hypochlora alba</i>						*				
<i>Melanoplus angustipennis</i>				0.01		0.03				0.03
<i>M. bivittatus</i>			0.05			*				
<i>M. confusus</i>			*			*				
<i>M. differentialis</i>				0.02						*
<i>M. femurrubrum</i>										0.01
<i>M. flavidus</i>									*	0.01
<i>M. foedus</i>						0.03				
<i>M. gladstoni</i>					*	0.02				0.02
<i>M. sanguinipes</i>						0.03		0.01	*	
<i>Phoetaliotes nebrascensis</i>				0.02		0.03				
Relative Use	*	*	*	*	*	0.02	*	*	*	*

TABLE I (Continued).

	<i>A. psyllostachya</i> D.C.	<i>Artemisia ludoviciana</i> Nutt.	<i>Aster ericoides</i> L.	<i>Chrysopsis villosa</i> (Pursh.) Nutt.	<i>Cirsium canescens</i> Nutt.	<i>Coryza canadensis</i> (L.) Cronq.	<i>Erigeron bellidistrum</i> Nutt.	<i>Helianthus annuus</i> L.	<i>H. petiolaris</i> Nutt.	<i>H. rigidus</i> (Cass.) Desf.
Plant Family	4	4	4	4	4	4	4	4	4	4
Relative Abundance	1.2	*	*	*	*	*	*	*	*	1.5
Grasshopper Species										
Gomphocerinae										
<i>Acrolophitus hirtipes</i>										
<i>Ageneotettix deorum</i>										
<i>Amphitornus coloradus</i>										
<i>Cordillacris occipitalis</i>										
<i>Eritettix simplex</i>										
<i>Mermiria bivittata</i>										
<i>Opeia obscura</i>										
<i>Parapomala wyomingensis</i>										
<i>Phlibostroma quadrimaculatum</i>										
<i>Psoloessa delicatula</i>										
Oedipodinae										
<i>Arphia conspersa</i>										
<i>A. pseudonietana</i>										
<i>Dissosteira carolina</i>										
<i>Hippiscus ocelote</i>										
<i>Spharagemon collare</i>										
<i>Trachyrhachys kiowa</i>										
<i>Trimerotropis citrina</i>		0.03								
Melanoplinae										
<i>Aeoloplides turnbulli</i>										
<i>Hesperotettix speciosus</i>	0.28			0.01			*	0.18	0.24	0.06
<i>H. viridis</i>		0.02	*					0.05		0.05
<i>Hypochlora alba</i>		0.94								
<i>Melanoplus angustipennis</i>	0.04	0.03				*				
<i>M. bivittatus</i>	0.07	0.12		0.06	0.04				0.04	*
<i>M. confusus</i>		0.10							0.02	
<i>M. differentialis</i>	0.04	0.02				0.04		0.02		
<i>M. femurrubrum</i>	0.15	0.01						0.04		
<i>M. flavidus</i>	0.12	0.01		0.05				*		0.02
<i>M. foedus</i>	0.03	0.06	0.02				*		*	*
<i>M. gladstoni</i>		0.12				*			*	
<i>M. sanguinipes</i>	0.01	0.02								0.04
<i>Phoetaliotes nebrascensis</i>		*								
Relative Use	0.03	0.05	*	*	*	*	*	0.01	0.01	*

TABLE I (Continued).

	<i>Kuhnia eupatorioides</i> L.	<i>Ratibida columifera</i> (Nutt.) Woot. and Standl	<i>Solidago missouriensis</i> Nutt.	<i>S. mollis</i> Bartl.	<i>Cryptantha celosoides</i> (Eastw.) Rayson	<i>Lappula redowskii</i> (Hornem.) Greene	<i>Lithospermum carolinense</i> (Walt.) MacMill	<i>L. incisum</i> Lehm.	<i>Eryssimum asperum</i> (Nutt.) D.C.	<i>Lesquerella ludoviciana</i> (Nutt.) Wats.
Plant Family	4	4	4	5	5	5	5	5	6	6
Relative Abundance	*	*	*	*	*	*	*	*	*	*
Grasshopper Species										
Gomphocerinae										
<i>Acrolophitus hirtipes</i>						0.23				0.14
<i>Ageneotettix deorum</i>										
<i>Amphitornus coloradus</i>										
<i>Cordillacris occipitalis</i>										
<i>Eritettix simplex</i>										
<i>Mermiria bivittata</i>										
<i>Opeia obscura</i>										
<i>Parapomala wyomingensis</i>										
<i>Phlibostroma quadrimaculatum</i>										
<i>Psoloessa delicatula</i>									0.01	
Oedipodinae										
<i>Arphia conspersa</i>										
<i>A. pseudonietana</i>	*									0.10
<i>Dissosteira carolina</i>										
<i>Hippiscus ocelote</i>										
<i>Spharagemon collare</i>										
<i>Trachyrhachys kiowa</i>										
<i>Trimerotropis citrina</i>										
Melanoplinae										
<i>Aeoloplides turnbulli</i>									0.01	0.01
<i>Hesperotettix speciosus</i>								*		
<i>H. viridis</i>	*			0.54						
<i>Hypochlora alba</i>									0.02	
<i>Melanoplus angustipennis</i>						0.02	*		*	0.04
<i>M. bivittatus</i>				*		0.02		0.02	0.02	*
<i>M. confusus</i>	0.01					0.07			0.02	
<i>M. differentialis</i>	0.01			0.02		0.01				
<i>M. femurrubrum</i>				0.05						
<i>M. flavidus</i>							0.01	*		0.01
<i>M. foedus</i>						*	*		0.05	0.02
<i>M. gladstoni</i>								0.02	0.11	0.06
<i>M. sanguinipes</i>		0.16	0.01	0.01	*		0.01		0.03	
<i>Phoetaliotes nebrascensis</i>							0.02		*	
Relative Use	*	*	*	0.02	*	0.01	*	*	0.01	0.01

TABLE I (Continued).

	<i>Chenopodium album</i> L.	<i>Kochia scoparia</i> (L.) Schrad.	<i>Amorpha canescens</i> Pursh.	<i>Astragalus crassicaarpus</i> Pursh.	<i>Oxytropis lambertii</i> Pursh.	<i>Petalostemon villasum</i> Nutt.	<i>Psoralea digitata</i> Nutt.	<i>Mentzelia nuda</i> (Pursh.) T. and S.	<i>Sphaeralcea coccinea</i> (Pursh.) Rydb.	<i>Calyptophus serrulatus</i> (Nutt.) Raven
Plant Family	7	7	8	8	8	8	8	9	10	11
Relative Abundance	*	*	*	*	*	*	*	*	*	*
Grasshopper Species										
Gomphocerinae										
<i>Acrolophitus hirtipes</i>						0.02		0.04		
<i>Ageneotettix deorum</i>										
<i>Amphitornus coloradus</i>										
<i>Cordillacris occipitalis</i>										
<i>Eritettix simplex</i>										
<i>Mermiria bivittata</i>										
<i>Opeia obscura</i>										
<i>Parapomala wyomingensis</i>										
<i>Phlibostroma quadrimaculatum</i>										
<i>Psoloessa delicatula</i>									*	0.01
Oedipodinae										
<i>Arphia conspersa</i>										
<i>A. pseudonietana</i>									0.03	
<i>Dissosteira carolina</i>	0.01									
<i>Hippiscus ocelote</i>										
<i>Spharagemon collare</i>									0.01	
<i>Trachyrhachys kiowa</i>										
<i>Trimerotropis citrina</i>									0.03	
Melanoplinae										
<i>Aeoloplides turnbulli</i>		0.05								
<i>Hesperotettix speciosus</i>					*		0.02		*	
<i>H. viridis</i>	0.13				*					
<i>Hypochlora alba</i>					0.01					
<i>Melanoplus angustipennis</i>				0.01	0.03	0.07			0.03	
<i>M. bivittatus</i>		0.06						0.03	0.01	
<i>M. confusus</i>					*		0.02		0.02	
<i>M. differentialis</i>		0.08			*					
<i>M. femurrubrum</i>	0.04				0.04					
<i>M. flavidus</i>				0.07	0.40	0.05			*	
<i>M. foedus</i>			0.02	0.01	0.06		0.02	0.03	0.11	
<i>M. gladstoni</i>				0.03	0.03	0.04				
<i>M. sanguinipes</i>					0.01	*			0.03	
<i>Phoetaliotes nebrascensis</i>		0.03							0.03	
Relative Use	*	*	*	*	0.02	*	*	*	0.01	*

TABLE I (Continued).

Plant Family	Unique but Unidentified					Flower Parts	Insect Parts	Unknown Forb	Unknown Grass
	R	S	T	U	V				
Grasshopper Species									
Gomphocerinae									
<i>Acrolophitus hirtipes</i>	0.54						0.02	0.04	0.01
<i>Ageneotettix deorum</i>							0.04		0.06
<i>Amphitornus coloradus</i>						*			
<i>Cordillacris occipitalis</i>									
<i>Eritettix simplex</i>									0.07
<i>Mermiria bivittata</i>								0.03	0.09
<i>Opeia obscura</i>							*		
<i>Parapomala wyomingensis</i>						0.04			0.04
<i>Phlibostroma quadrimaculatum</i>								0.02	
<i>Psoloessa delicatula</i>								0.04	0.02
Oedipodinae									
<i>Arphia conspersa</i>							0.03	0.08	0.03
<i>A. pseudonietana</i>							0.07	0.02	0.01
<i>Dissosteira carolina</i>						0.06	0.03	0.01	0.06
<i>Hippiscus ocelote</i>							0.13		
<i>Spharagemon collare</i>							0.07		0.22
<i>Trachyrhachys kiowa</i>									
<i>Trimerotropis citrina</i>						0.04	0.21	0.03	
Melanoplinae									
<i>Aeoloplides turnbulli</i>	0.02			0.02	0.63		0.02	0.08	0.02
<i>Hesperotettix speciosus</i>						*		0.07	*
<i>H. viridis</i>							0.06		
<i>Hypochlora alba</i>							*	0.03	
<i>Melanoplus angustipennis</i>						0.26	0.08	0.05	0.05
<i>M. bivittatus</i>		0.05	*				0.08	0.06	
<i>M. confusus</i>							0.17	0.04	
<i>M. differentialis</i>	0.04		0.04				0.01	0.13	0.06
<i>M. femurrubrum</i>		0.27				0.04	0.01	0.16	0.15
<i>M. flavidus</i>						0.07		0.06	0.06
<i>M. foedus</i>						0.07	0.14	0.11	0.08
<i>M. gladstoni</i>							0.12	0.08	*
<i>M. sanguinipes</i>						*	0.06	0.10	0.03
<i>Phoetaliotes nebrascensis</i>						0.02	0.02	0.05	0.07
Relative Use	0.02	0.01	*	*	0.02	0.02	0.05	--	--

melanoplines. Compared with the distribution of diet breadths from other sites, those at Arapaho Prairie have a larger than expected average. Average diet breadths of grasshoppers from this site are among the highest of all sites measured (Joern, 1983).

Comparison with North Platte

Grasshopper diets have also been determined from a mixed-grassland pasture near North Platte, Nebraska (Mulkern et al., 1969; Pruess, 1969 and 1970), approximately 100 km from Arapaho Prairie. Very different results were observed. The average diet breadth at North Platte was 5.9 compared with 8.4 at Arapaho Prairie (Joern, 1983); the distribution of diet breadths for North Platte (Fig. 1) is significantly different from Arapaho Prairie (Mann-Whitney *U*-test, $p < 0.005$), also shown in Figure 1.

In addition, Pruess (1969) carefully examined the diet of *Poetaliotes nebrascensis*. At North Platte, *P. nebrascensis* primarily feeds on *Agropyron smithii* (65% of the diet) as well as *Calamovilfa longifolia* (6%) and small amounts of several other grasses. However, this species has a very different diet at Arapaho Prairie (Table I); six grass and sedge species are included as at least 5% of the diet, and no plant constitutes more than 18% of the total diet (*A. smithii* constitutes 11% of the diet). Pruess (1969) also examined diet preferences in the North Platte population of *P. nebrascensis*. *Agropyron smithii* was a highly ranked host plant in paired-preference studies although the present comparison suggests that preference alone is not a sufficient reason for inclusion into the diet. Although *A. smithii* is included in the diet of *P. nebrascensis* at Arapaho Prairie and the grass is present at the site, great differences in degree of inclusion in the diet remain. Perhaps the populations of this plant differ in palatability as Pruess (1970) observed for populations of big bluestem (*Andropogon gerardi*) from North Platte versus Manhattan, Kansas, when fed on by *Ageneotettix deorum*. The much larger range of host plants in the Arapaho Prairie population also needs explanation. Some possible explanations for the observed general patterns have been suggested (Joern, 1979 and 1983).

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