

Grasshopper Food Habits within a Shrub-Steppe Community

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Summary. Results from a dietary analysis of eight grasshopper species inhabiting a shrub-steppe community in southeastern Washington showed that 15 vascular plant species served as food items. Several plant species occurred at higher frequencies in the diet samples than in the plant community. Big sagebrush (*Artemisia tridentata*) was the most frequently selected plant species, followed by turpentine cymopterus (*Cymopterus terebinthinus*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and Carey's balsamroot (*Balsamorhiza careyana*).

Introduction

Grasshoppers are a conspicuous faunal component in arid lands of southeastern Washington. Since they are predominantly herbivores, their presence in large numbers exerts a significant destructive influence on desert vegetation. The earlier conclusion that an opportunistic feeding strategy is typical of grasshoppers has been replaced by the knowledge that most species exhibit varying degrees of selectivity (Mulkern, 1967). The nature of this specificity in food plant selection largely determines the effect on flora.

An earlier study (Rogers and Uresk, 1974) examined food plant selections of the migratory grasshopper, *Melanoplus sanguinipes* (F.), within a cheatgrass (*Bromus tectorum*) community on the Hanford Reservation. This paper examines food niche breadths and overlaps in diets of eight grasshopper species collected from a shrub-steppe community. The species studied were *Ageneotettix deorum* (Scudder), *Conozoa wallula* (Scudder), *Hesperotettix viridis* (Thomas), *Melanoplus cinereus* Scudder, *Melanoplus yarrowii* (Thomas), *Oedaleonotus enigma* (Scudder), *Trimerotropis caeruleipennis* Bruner, and the northwestern shield-back katydid, *Apote notabilis* Scudder.

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Richland, Washington, as part of a general study initiated to document food habits and transfer pathways through major consumer populations.

Study Area

Grasshoppers were collected for dietary analysis from a sagebrush-cheatgrass community located about 223 m above mean sea level. The dominant shrub was big sagebrush (*Artemisia tridentata*). It had a density of ca. 3720 plants per ha, relative frequency (%FO) of 8%, and covered about 26% of the area (Table 1). Common rabbitbrush (*Chrysothamnus nauseosus*) and green rabbitbrush (*C. viscidiflorus*) were also present, but less prevalent. Twenty-four herbaceous plant species covered ca. 37% of the area. Of these, 17 were recorded at a frequency of less than 1%. Two species of annual grass, cheatgrass (*Bromus tectorum*) and six-weeks fescue (*Festuca octoflora*), covered a combined area of 19%. Sandberg's bluegrass (*Poa sandbergii*), a perennial, was less abundant (%FO=5, %C=2). Western tansymustard (*Descurainia pinnata*) was the most abundant (%FO=18, %C=8) annual forb, followed by microsteris (*Microsteris gracilis*) (%FO=14, %C=3), matted cryptantha (*Cryptantha circumscissa*) (%FO=10, %C=2), and winged cryptantha (*Cryptantha pterocarya*) (%FO=3, %C<1).

The climate of the region is arid with hot, dry summers and cold winters. Annual precipitation averages 17 cm (Rickard, 1972) with most occurring from October through May. From June through September, there is little rain and significant dehydration occurs in most plant species. Those species retaining moisture are often very attractive to herbivores and provide a source of food and water. The plant community during the summer thus undergoes a marked change in vegetative quality and quantity and species composition.

Materials and Methods

Insects for diet analysis were collected biweekly between 27 June and 8 August 1974. Adult specimens were collected with a standard aerial insect net and immediately preserved in 95% ETOH. A microscope slide mount was prepared from the crop contents of each grasshopper. Plant species were identified as described by Rogers and Uresk (1974). Determinations were based on structural characteristics of epidermal cells specific to each plant species (comparison was made to a reference collection containing all plant taxa present in the study area). Twenty microscope fields were read per slide. Frequency of occurrence was calculated for each food item present based on the number of fields containing a particular food item. Frequency was converted to relative frequency and appears in Table 1 as %FC.

Diet similarity, as an index of dietary overlap, was evaluated using Kulczynski's formula (Oosting, 1956),

$$S = \frac{2 \sum_{i=1}^s W_i(100)}{\sum_{i=1}^s a_i + b_i}$$

where a_i represents the mean percentage of food item i in the diet of species a , b_i represents the mean percentage of food item i in the diet of species b , and w_i represents a_i if $a_i \leq b_i$ or b_i if $b_i \leq a_i$. A mean was calculated for these indices comparing the diet of each grasshopper

Table 1. Plant taxa; common names, habitat frequency of occurrence (%FO); canopy cover (%C) (data from Uresk et al., 1975; Cline et al., 1975) and frequency of diet composition (%FC) (All grasshopper species combined). Plant nomenclature follows Hitchcock and Cronquist (1973)

Taxa	Common name	%FO	%C	%FC
Annual grasses				
<i>Bromus tectorum</i> L.	Cheatgrass	20	15	<1
<i>Festuca octoflora</i> Walt.	Six-weeks fescue	16	4	0
Perennial grasses				
<i>Poa sandbergii</i> Vasey	Sandberg's bluegrass	5	2	<1
<i>Stipa comata</i> Trin. & Rupr.	Needle-and-thread grass	<1	<1	<1
<i>Agropyron spicatum</i> (Pursh) Scribn. & Smith	Bluebunch wheatgrass	<1	<1	0
Perennial forbs				
<i>Oenothera pallida</i> Lindl.	White-stemmed Evening Primrose	<1	<1	0
<i>Cymopterus terebinthinus</i> (Hook.) T & G	Turpentine cymopterus	<1	<1	15
<i>Erigeron filifolius</i> Nutt.	Thread-leaved fleabane	<1	<1	0
<i>Calochortus macrocarpus</i> Dougl.	Green-banded star-tulip	<1	<1	0
<i>Mentzelia albicaulis</i> Dougl.	White-stemmed mentzelia	<1	<1	0
<i>Phlox longifolia</i> Nutt.	Long-leaved phlox	<1	<1	0
<i>Brodiaea douglassii</i> Wats.	Douglas' brodiaea	<1	<1	0
<i>Comandra umbellata</i> (L.) Nutt.	Bastard toad-flax	<1	<1	0
<i>Balsamorhiza careyana</i> Gray	Carey's balsamroot	<1	<1	13
<i>Achillea millefolium</i> L. ^a	Common yarrow	0	0	<1
Annual forbs				
<i>Descurainia pinnata</i> (Walt.) Britt.	Western tansymustard	18	8	5
<i>Cryptantha circumscissa</i> (H. & A.) Johnst.	Matted cryptantha	10	2	<1
<i>Sisymbrium altissimum</i> L.	Jim Hill mustard	<1	<1	7
<i>Salsola kali</i> L.	Russian thistle	<1	<1	<1
<i>Cryptantha pterocarya</i> (Torr.) Greene	Winged cryptantha	3	<1	0
<i>Microsteris gracilis</i> (Hook.) Greene	Microsteris	14	3	0
<i>Phacelia linearis</i> (Pursh) Holz.	Narrow-leaved phacelia	<1	<1	0
<i>Amsinckia lycopsoides</i> Lehm.	Tarweed fiddleneck	<1	<1	1
<i>Erodium cicutarium</i> (L.) L' Her.	Filaree	<1	<1	0
Shrubs				
<i>Artemisia tridentata</i> Nutt.	Big sagebrush	8	26	41
<i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.	Green rabbitbrush	<1	<1	16
<i>Chrysothamnus nauseosus</i> (Pall.) Britt. ^a	Common rabbitbrush	<1	<1	<1
<i>Atriplex spinosa</i> (Hook.) Collotzi ^a	Spiny hopsage	0	0	<1
Total Taxa		28	15	

^a Plant species identified in diet study but not found in vegetation analysis

species with that of every other species. Analysis of variance was used to determine if the means were statistically different, and Student-Newman-Keuls Multiple-range Test used to test for difference between means.

Spearman's rank correlation coefficient (Wolf, 1968) was used to estimate differences between the orders of abundance of foods in the diets of the 8 species.

Vegetation analysis data was taken from Uresk et al. (1975) and Cline et al., 1975. Their shrub data was obtained by examining all individuals rooted within a 10 × 50 m study plot. Herbaceous species were examined by reading fifty 2 × 5 decimeter quadrats spaced at 1-m intervals along a 50 m line transect.

Results and Discussion

Crop contents of 576 grasshoppers representing 8 species were examined and a total of 16 plant taxa identified (Table 2). In all cases, the 'unknown' category

Table 2. Relative frequency of plant species in diets of 8 species

Plant species	Grasshopper species ^a							
	APNO	TRCA	COWA	MECI	MEYA	OEEN	AGDE	HEVI
Annual Grasses								
<i>Bromus tectorum</i>							3	
Perennial grasses								
<i>Poa sandbergii</i>					2			
<i>Stipa comata</i>	<1	8	4				3	
Perennial forbs								
<i>Cynopterus terebinthinus</i>	34			6	15	2		<1
<i>Balsamorhiza careyana</i>	<1	25	73	<1	22	3		
<i>Achillea millefolium</i>				2	<1			
Annual forbs								
<i>Descurainia pinnata</i>	3	12	3	1	7	4		<1
<i>Cryptantha circumscissa</i>	<1					<1	<1	
<i>Sisymbrium altissimum</i>	13			5	3	2		
<i>Salsola kali</i>						<1	<1	<1
<i>Amsinckia lycopsoides</i>		6				<1	<1	
Shrubs								
<i>Artemisia tridentata</i>	18	6	<1	61	12	47	4	
<i>Chrysothamnus viscidiflorus</i>	15		3	6	6	2	1	76
<i>Chrysothamnus nauseosus</i>				<1	<1	<1	3	
<i>Atriplex spinosa</i>				<1		<1		
Other								
Lichen	15	42	16	18	27	36	81	21
Unknown	2	<1		<1	<1	<1	3	1
Number of crops examined	61	17	38	124	137	111	36	52
Number of food types utilized (excluding the unknown category)	9	6	6	10	13	11	9	3

^a APNO = *Apote notabilis* Scudder; TRCA = *Trimerotropis caeruleipennis* Bruner; COWA = *Conozoa wallula* (Scudder); MECI = *Melanoplus cinereus* Scudder; MEYA = *Melanoplus yarrowii* (Thomas); OEEN = *Oedaleonotus enigma* (Scudder); AGDE = *Ageneotettix deorum* (Scudder); HEVI = *Hesperotettix viridis* (Thomas)

constituted 3% or less of the diet. The food niche breadth of the eight grasshopper species varied from a maximum of 12 vascular plant species recorded from *M. yarrowii* to a minimum of two species from *H. viridis*. Thirteen of the 24 species of herbaceous vascular plants recorded in Table 1 were not encountered in any of the eight grasshoppers' diets, although three of them were major components of the flora, e.g., six-weeks fescue, winged cryptantha, and microsteris. Three of the common plant species, cheatgrass, Sandberg's bluegrass, and matted cryptantha, were consumed at very low levels. The habitat frequency of four heavily foraged plant species was 1% or less. These species included turpentine cymopterus, Carey's balsamroot, Jim Hill mustard, and green rabbitbrush.

Grasses were not found to constitute a major portion of the overall grasshopper diet (Table 1). Needle-and-thread was consumed by *T. caeruleipennis*, *A. deorum*, and *C. wallula* at a higher level than its habitat frequency and was present in the diet of *A. notabilis* (Table 2). The small amount of grass consumed by *A. deorum* indicates a somewhat atypical food base for this normally granivorous species (Banfill and Brusven, 1973; Mulkern et al., 1969; Ueckert et al., 1972). It also contained the highest cryptogam frequency which correlates well with observations reporting a significant level of detritus feeding (Mulkern et al., 1969; Lavigne and Pfadt, 1964; Banfill and Brusven, 1973).

Two species of perennial forbs were widely utilized, although in both cases their habitat frequency was less than 1%. Turpentine cymopterus was found in the diets of 5 of the 8 species and Carey's balsamroot was utilized by all but two species. Western tansymustard was consumed by 7 of the 8 species, although the overall diet frequency was far below its habitat frequency. Jim Hill mustard was utilized by four species.

Big sagebrush and green rabbitbrush were consumed by seven of the eight grasshopper species, and each served as a major food source for one species. *Melanoplus cinereus* was usually found on the foliage of big sagebrush and had a diet frequency of 61% for that species. Banfill and Brusven (1973) reported this species feeding on *Artemisia ludoviciana* along the breaks of the Salmon River in Idaho. On the other hand, *H. viridis* was found almost exclusively on green rabbitbrush and had a diet frequency of 76% for this species. *Cryptogams* provided the only other major food source. Other studies have also shown that *H. viridis* is selective in its feeding behavior. At North Platte, Nebraska, it is reported to feed primarily on *Gutierrezia sarothrae* and *Aster oblongifolius* (Mulkern et al., 1969). Brooks (1958) reported that in the Canadian prairie provinces, *Gutierrezia* sp. was the major food source, but *Solidago* sp., *Helianthus* sp., *Grindelia* sp., and *Aster* sp. were also eaten. In a Montana study (Anderson and Wright, 1952), *H. viridis* was closely associated with *Gutierrezia* sp., but also ingested *Solidago rigida*, *Chrysothamnus neuseosus*, and *Grindelia squarrosa*.

Scavenging was observed in only one species, the tettigoniid *A. notabilis*. This species, which is largely nocturnal in contrast to the diurnal grasshoppers, was often observed feeding on dead insects (including members of its own species) and on other detritus. This habit was particularly noticeable along roadways.

The combined results for all grasshopper species (Table 1) show that the diet frequency of 41% for big sagebrush is more than twice that of any other

vascular plant. These results correct the recent statement by Daubenmire (1975) that the foliage of big sagebrush is not eaten by grasshoppers. He states that grasshoppers congregate on big sagebrush at night, roosting on the canopy. We confirmed this and also found that during the heat of the day many species of grasshoppers sit on big sagebrush to avoid the high temperatures of exposed soil surface areas.

Similarity indices based on Kulczynski's formula are presented in Table 3. High indices indicate a large overlap in the diets of two species, such as with the value of 73.7 calculated for *M. cinereus* and *O. enigma*. The low index of 18.6 calculated for *H. viridis* and *C. wallula* indicates little overlap between diets.

The means of the similarity indices are ranked (last column, Table 3) according to degree of dietary overlap. Means ranged from 47.5 to 24.7. Species with the greatest dietary overlap were *M. yarrowii* and *O. enigma*, while *C. wallula* and *H. viridis* were most unique.

The amount of dietary overlap for grasshoppers was similar to that reported by Ueckert and Hansen (1971) for grasshoppers inhabiting northeastern Colorado. Although individual similarity indices had a greater range in Colorado (91 to 4 vs. 74 to 19), the mean of the means for diet overlap for all grasshopper species from the two areas were similar (36.7 for 8 species reported here, and 26.4 for 14 grasshopper species in the Colorado study). The greater divergence in the similarity indices in the Colorado study is likely due to the broader selection of plant species available and more variety in species of grasshoppers.

Grasshoppers in the two areas are exposed to different competitive pressures. Peak grasshopper density in Colorado is reached during the summer growing season when vegetation is lush. The eastern Washington population, in contrast, first appears near or after the climax of the spring growing season and matures during the increasingly arid summer. Early instar nymphs find succulent vegetation readily abundant, but later instars and adults are mostly left with dehydrated food plants. Certain plant species, such as turpentine cymopterus, big sagebrush, and rabbitbrush, have the capacity to retain moisture and are heavily utilized as forage later in the summer. These plants provide a large bulk of the food

Table 3. Similarity indices for the diets of 8 grasshopper species from S.E. Washington. The mean of all indices for each species is given in the last column

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	\bar{X}
MEYA (1)		54.3	63.3	47.0	56.2	38.1	44.8	29.1	47.5 a ^a
OEEN (2)			49.5	73.7	42.3	44.9	24.3	23.5	44.6 ab
TRCA (3)				26.4	25.4	51.2	48.7	22.0	40.9 bc
MECI (4)					50.4	26.4	20.6	24.0	38.3 bcd
APNO (5)						24.4	21.9	30.7	35.9 cd
AGDE (6)							21.4	24.7	33.0 de
COWA (7)								18.6	28.6 ef
HEVI (8)									24.7 f

^a Mean followed by similar letters are not significantly different ($P=0.05$)

Table 4. Spearman's rank correlation coefficients for food selection among the 8 grasshopper species studied in southeast Washington. Significance levels are indicated

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
MEYA (1)		0.79 ^b	0.36	0.64 ^a	0.68 ^b	0.03	0.50	0.08
OEEN (2)			0.41	0.65 ^a	0.69 ^b	0.11	0.47	-0.04
TRCA (3)				-0.09	-0.23	0.06	0.73 ^a	-0.37
MECI (4)					0.75 ^b	0.14	0.03	0.08
APNO (5)						0.13	-0.23	0.06
AGDE (6)							0.00	0.07
COWA (7)								-0.17
HEVI (8)								

^a = $P < 5\%$

^b = $P < 1\%$

and serve as a major source of water. At summer's end, turpentine cymopterus is virtually stripped of its leaves and much of the stem is also consumed.

Further analysis of the diets of the 8 species as calculated by Spearman's rank order statistic indicates a significant correlation in the order of food selection of several species (Table 4). The species with the lowest correlations, and thus the most unique diets, were *Ageneotettix deorum* and *Hesperotettix viridis*. Neither of the two species showed significant correlation with other species.

We recognize that the apparent selection of particular food plants may represent selection for special microhabitat conditions. Irrespective of the reasons, food partitioning does occur between some grasshopper populations occupying this semiarid region. These differential feeding patterns are an important consideration when assessing transfer pathways through native consumer populations.

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