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ABSTRACT The diets of 13 species of darkling beetles inhabiting shrub–steppe communities of southcentral Washington were analyzed. Forty-seven vascular plant species, including 7 grasses, 34 forbs, and 6 shrubs, were fed upon. Cluster analysis was used to determine the extent of overlap in food habits among beetle species. The beetle species were separated into five food preference groups. Partitioning of food resources may act to refine niche space of these beetles.

KEY WORDS Insecta, darkling beetles, dietary niches, Tenebrionidae

DARKLING BEETLES are a conspicuous part of the invertebrate fauna in the semiarid regions of the western United States. Their abundance in shrub–steppe and desert regions (Rickard & Haverfield 1965, Hinds & Rickard 1973, Rogers & Rickard 1975, Sheldon & Rogers 1984) suggests that they play an important role in the functioning of these ecosystems.

Understanding the diets of major consumers is essential in understanding ecosystem functioning, because consumption serves as a control point for materials entering transport pathways. Our objective was to describe the dietary relationships of darkling beetles occupying shrub–steppe communities of the Hanford Site in southcentral Washington.

Materials and Methods

This research was conducted on lands owned by the U.S. Department of Energy and known administratively as the Hanford National Environmental Research Park (NERP). The Hanford NERP extends over 148,000 ha (570 square miles) of relatively pristine shrub–steppe vegetation in southcentral Washington. Nine study sites were selected within major biotic communities (Table 1); they have been described by Sheldon & Rogers (1984).

Twenty-five pitfall traps were placed in a straight line at 5-m intervals at each study site. Each trap was a metal can (9 by 9 cm) buried flush with the soil surface. A 5% formalin solution maintained to within 2.5 cm of the rim of the traps quickly killed the beetles and stopped digestion. The traps were emptied weekly from March through October during a 2-yr period. The digestive tract was removed from each beetle, cleared with Hertwig's solution, and prepared for microscopic analysis as described by Sparks & Malechek (1968), Hansen & Flinders (1969), and Rogers & Uresk (1974).

We prepared reference slides of all plant species known to occur within the study sites. Plant samples (including leaves, stems, and flowers) were dried, partially ground (1 mm screen size), and mounted separately. Prepared slides of beetle digestive tracts were sent to the Composition Analysis Laboratories, Colorado State University, Ft.

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Table 1. Study sites

Study site	Dominant plant community: Common name	Scientific name	Elevation, m	Precipitation, cm[a]
1	Cheatgrass (upper oldfield)	*Bromus tectorum*	533	26
2	Cheatgrass (lower oldfield)	*Bromus tectorum*	323	21
3	Sagebrush–bunchgrass	*Artemisia tridentata–Agropyron spicatum*	330	23
4	Greasewood–cheatgrass	*Sarcobatus vermiculatus–Bromus tectorum*	210	17
5	Winterfat–bluegrass	*Eurotia lanata–Poa sandbergii*	206	20
6	Hopsage–cheatgrass	*Atriplex spinosa–Bromus tectorum*	158	18
7	Sagebrush–bluegrass	*Artemisia tridentata–Poa sandbergii*	198	15
8	Sagebrush–bluegrass	*Artemisia tridentata–Poa sandbergii*	192	15
9	Sagebrush–bluegrass	*Artemisia tridentata–Poa sandbergii*	220	15

[a] From Stone et al. 1972.

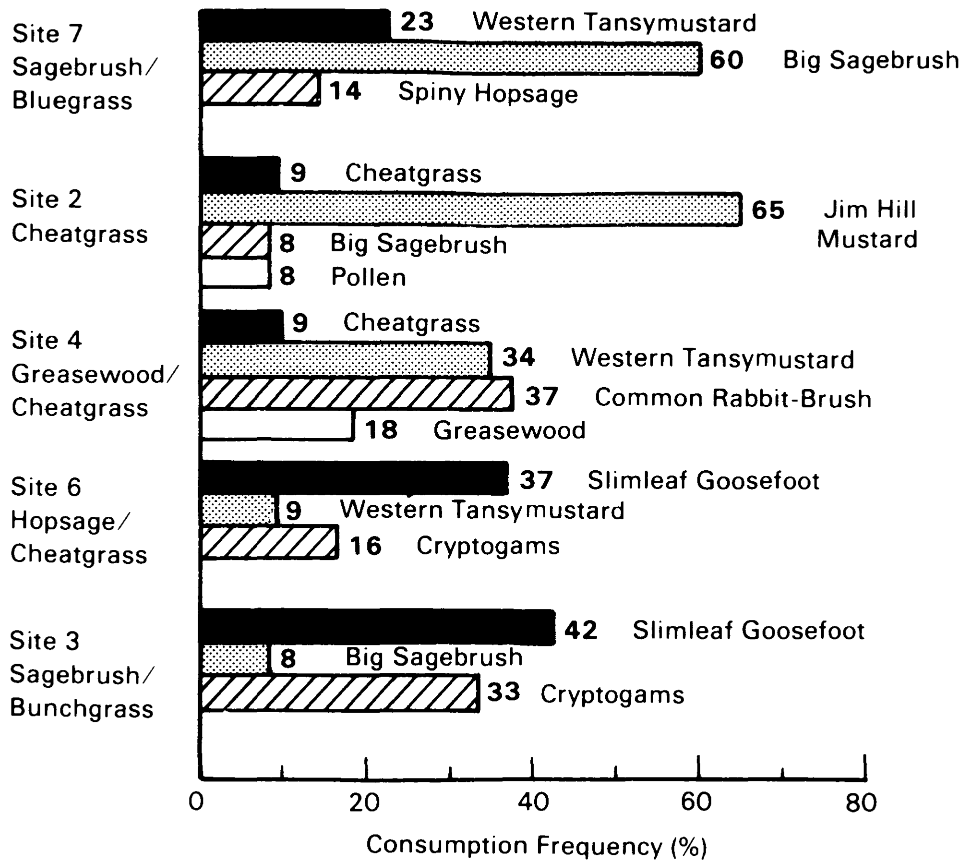

Fig. 1. Consumption frequency (%) of major plant species by *C. setosa*.

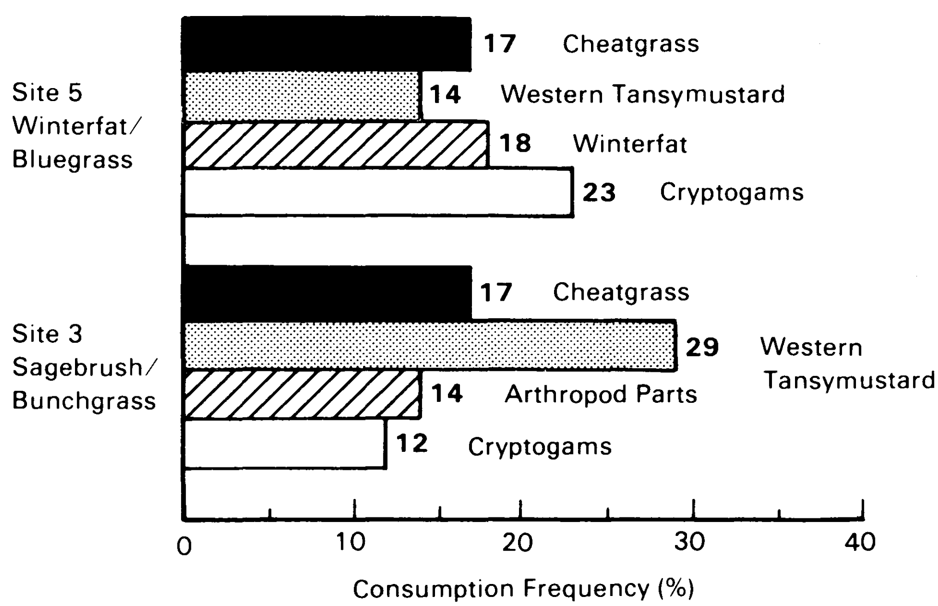

Fig. 2. Consumption frequency (%) of major plant species by *E. granulata*.

Table 2. Relative frequency (%) of plant species in diets of 13 darkling beetles[a]

		ELGR	ELHI	ELHU	ELOB	ELNI	ELNO	EUMU	PHDE	STPU	BLSP	COSE	OXHI	CORE
Grasses														
Agropyron spicatum (Pursh) Scribn. and Smith	Bluebunch wheatgrass	<1	0	0	0	0	0	0	<1	0	0	0	0	0
Bromus tectorum L.	Cheatgrass	18	4	1	24	4	5	3	6	23	6	8	2	14
Festuca octoflora Walt.	Slender fescue	0	0	0	0	1	0	0	<1	0	11	0	0	0
Poa cusickii Vasey	Cusick's bluegrass	1	<1	0	0	0	0	0	<1	1	0	<1	0	0
Poa sandbergii Vasey	Sandberg's bluegrass	1	1	0	0	1	<1	0	3	0	0	0	0	0
Stipa sp.	Needle and thread	1	<1	0	3	0	2	3	<1	0	0	0	0	8
Unknown grass		<1	1	<1	0	1	5	2	<1	<1	11	1	5	<1
Forbs														
Ambrosia acanthicarpa Hook.	Bursage ragweed	0	<1	0	0	0	0	0	2	0	0	0	0	0
Amsinckia sp.	Fiddleneck	0	<1	0	0	0	0	2	3	<1	0	0	0	0
Antennaria dimorpha (Nutt) T. and G.	Low pussy-toes	0	0	0	0	1	0	0	0	0	0	0	0	0
Astragalus sp.	Locoweed	<1	0	0	0	0	0	0	0	1	0	0	0	0
Balsamorhiza careyana Gray	Carey's balsamroot	0	0	0	0	0	0	2	0	0	0	0	0	0
Calochortus macrocarpus Dougl.	Sagebrush mariposa	0	0	0	0	0	<1	0	0	0	0	0	0	0
Castilleja sp.	Paintbrush	0	<1	0	0	1	0	0	1	0	0	<1	0	0
Chenopodium leptophyllum (Moq.) Wats.	Slimleaf goosefoot	0	3	1	0	5	1	0	<1	3	0	19	0	2
Chenopodium sp.	Lambs quarters	0	<1	0	0	0	0	0	<1	0	0	0	0	0
Crepis atrabarba Heller	Slender hawksbeard	<1	0	0	17	4	0	0	0	0	0	0	0	0
Cryptantha sp.	Cryptantha	0	<1	0	0	0	1	<1	3	0	0	0	0	0
Cymopterus terebinthinus (Hook.) T. and G.	Turpentine cymopterus	0	0	0	7	0	0	0	0	0	0	0	0	0
Descurainia pinnata (Walt.) Britt.	Western tansymustard	15	18	0	<1	15	6	22	17	8	6	8	0	37
Draba verna L.	Spring whitlow-grass	<1	<1	0	0	<1	0	0	1	1	0	0	0	1
Erigeron filifolius Nutt.	Thread-leaf fleabane	0	<1	0	0	0	0	<1	1	0	0	0	0	0
Erysimum asperum (Nutt.) DC.	Rough wallflower	4	1	0	0	<1	0	0	2	0	0	0	0	0
Helianthus sp.	Sunflower	0	<1	0	0	<1	0	0	5	1	0	0	2	0
Lappula redowskii (Hornem.) Greene	Western stickseed	0	0	0	0	0	0	0	0	0	0	0	0	0
Lomatium macrocarpum (Nutt.) Coult. and Rose	Large-fruit lomatium	0	1	0	0	0	0	0	0	0	0	0	0	0
Lupinus sp.	Lupine	0	<1	0	0	0	0	0	0	0	0	0	0	0
Microsteris gracilis (Hook.) Greene	Pink microsteris	0	0	0	0	0	0	0	<1	1	0	0	0	0
Phacelia linearis (Pursh.) Holtz.	Threadleaf phacelia	<1	0	0	0	0	0	0	0	0	0	0	0	0
Plantago patagonica Jacq.	Indian-wheat	0	<1	0	0	0	0	0	0	0	0	0	0	0
Polemonium micranthum Benth.	Littlebells polemonium	0	0	0	0	0	0	1	1	<1	0	<1	0	0
Psoralea lanceolata Pursh.	Lance-leaf scurf-pea	0	0	0	0	0	0	0	<1	0	0	0	0	1
Salsola kali L.	Russian thistle	4	3	2	26	2	4	0	1	0	0	1	1	0
Sisymbrium altissimum L.	Jim Hill mustard	1	1	0	0	0	<1	1	4	16	6	18	0	<1
Sphaeralcea munroana (Dougl.) Spach	Munro's globe-mallow	0	17	0	0	6	0	<1	1	0	0	<1	0	2
Taraxacum officinale Weber	Common dandelion	0	0	0	6	0	0	0	0	0	0	0	0	0
Townsendia florifer (Hook.) Gray	Showy townsendia	0	0	0	<1	0	<1	0	1	0	11	0	0	0
Tragopogon dubius Scop.	Yellow salsify	0	0	0	0	0	0	0	0	0	0	1	0	0
Compositae	Aster family	0	0	0	0	0	<1	<1	<1	<1	0	2	<1	0
Liliaceae	Lily family	0	<1	0	0	0	0	0	<1	<1	0	<1	2	0
Unknown forbs		2	1	0	<1	1	1	2	1	1	11	2	0	6
Shrubs														
Artemisia tridentata Nutt.	Big sagebrush	3	5	51	3	12	16	50	9	3	11	12	11	14
Atriplex spinosa (Hook.) Collotzi	Spiny hopsage	<1	2	2	1	0	5	1	2	1	0	2	0	0

Table 2. Continued.

		ELGR	ELHI	ELHU	ELOB	ELNI	ELNO	EUMU	PHDE	STPU	BLSP	COSE	OXHI	CORE
Chrysothamnus nauseosus (Pall.) Britt.	Common rabbit-brush	1	<1	36	0	2	4	3	0	<1	0	3	5	0
Chrysothamnus viscidiflorus (Hook.) Nutt.	Green rabbit-brush	0	<1	0	0	0	0	1	0	0	0	<1	0	0
Eurotia lanata (Pursh.) Moq.	Winterfat	11	9	0	0	16	5	<1	12	14	0	2	0	0
Sarcobatus vermiculatus (Hook.) Torr.	Black greasewood	<1	<1	4	<1	7	1	0	7	11	0	2	5	1
Miscellaneous														
Arthropod parts		7	14	2	6	9	9	2	1	<1	17	3	19	7
Cryptogams		23	8	1	7	9	30	3	17	13	0	12	46	4
Hair		0	0	0	0	0	0	0	<1	0	0	0	0	0
Seeds		1	4	0	0	3	0	1	<1	<1	0	1	0	<1
Pollen		3	3	0	0	0	5	0	0	0	11	3	0	1
Number of digestive tracts examined		73	124	18	13	49	38	70	200	127	27	97	37	88
Number of foods used		24	34	10	14	22	21	21	36	23	10	24	11	16

[a] ELGR, *Eleodes granulata* LeConte; ELHI, *Eleodes hispilabris* Blaisdell; ELHU, *Eleodes humeralis* LeConte; ELOB, *Eleodes obscura* Say; ELNI, *Eleodes nigrina* Blaisdell; ELNO, *Eleodes novoverrucula* Boddy; EUMU, *Eusattus muricatus* LeConte; PHDE, *Philolithus densicollis* Horn; STPU, *Stenomorpha puncticollis* LeConte; BLSP, *Blapstinus* species (both *B. discolor* Horn and *B. substriatus* Champion); COSE, *Coniontis setosa* Casey; OXHI, *Oxygonodera hispidula* Horn; CORE, *Conisattus rectus* Boddy. Plant names are from Hitchcock & Cronquist (1973).

Collins, together with plant reference slides for analysis. Twenty microscope fields were read from each slide, and the frequency of occurrence of each plant species was calculated (Table 2).

Niche overlap was calculated for each species based on food items found in the gut analysis (see Pianka 1975, Wiens & Rotenberry 1979) from the formula:

$$0 = \frac{\sum_{i}^{n} p_i q_i}{\sqrt{\sum_{i}^{n} p_i^2 \sum_{i}^{n} q_i^2}}$$

where p_i is the relative frequency of a diet item in the diet of a given taxon, and q_i is the relative frequency of a diet item in another taxon. Cluster analysis was used to compare dietary niche overlap among beetle species (Hartigan 1975).

Results

Thirteen species of darkling beetles in eight genera were collected, and their food was analyzed. Digestive tracts of 960 individuals were examined, and a total of 52 different food items were recorded: 7 grass, 34 forb, 6 shrub, and 5 miscellaneous food types (Table 2). Four beetle species were abundant on five sites, three on three sites, one on two sites, and five on only one site. Comparisons of foods habits of species occupying more than one study location are shown in Fig. 1–8. Only those plant species consumed at a frequency greater than 7% are included.

Blapstinus substriatus Champion and *B. discolor* Horn. Ten food plants were identified in *Blapstinus* diets (Table 2). Fragments of arthropod parts comprised 17% of the diet. These are small beetles, and some arthropod fragments may be artifacts associated with our dissection and mounting. Plant pollen, big sagebrush, slender fescue, needle-and-thread grass, *Townsendia*, and unknown forbs each comprised 11% of the diet. *Blapstinus* was abundant only in the old field communities, and diets were analyzed only at the lower old-field community (Site 2).

Coniontis setosa Casey. Twenty-four different food items were ingested by this beetle (Table 2). The most frequent were slimleaf goosefoot (19%), Jim Hill mustard (18%), big sagebrush (12%), and cryptogams (12%). Food selection changed at different sites (Fig. 1). Big sagebrush was frequently consumed at the sagebrush–bluegrass community (Site 7) but accounted for less than 10% of the diet in other areas. Major food plants at other sites were Jim Hill mustard in the lower old field (Site 2); western tansymustard and rabbitbrush in the greasewood community (Site 4); and slimleaf goosefoot and cryptogams in the hopsage–cheatgrass community (Site 6).

Conisattus rectus Boddy. *C. rectus* (=*C. nelsoni* [Doyen 1984]) was abundant only in the sagebrush–

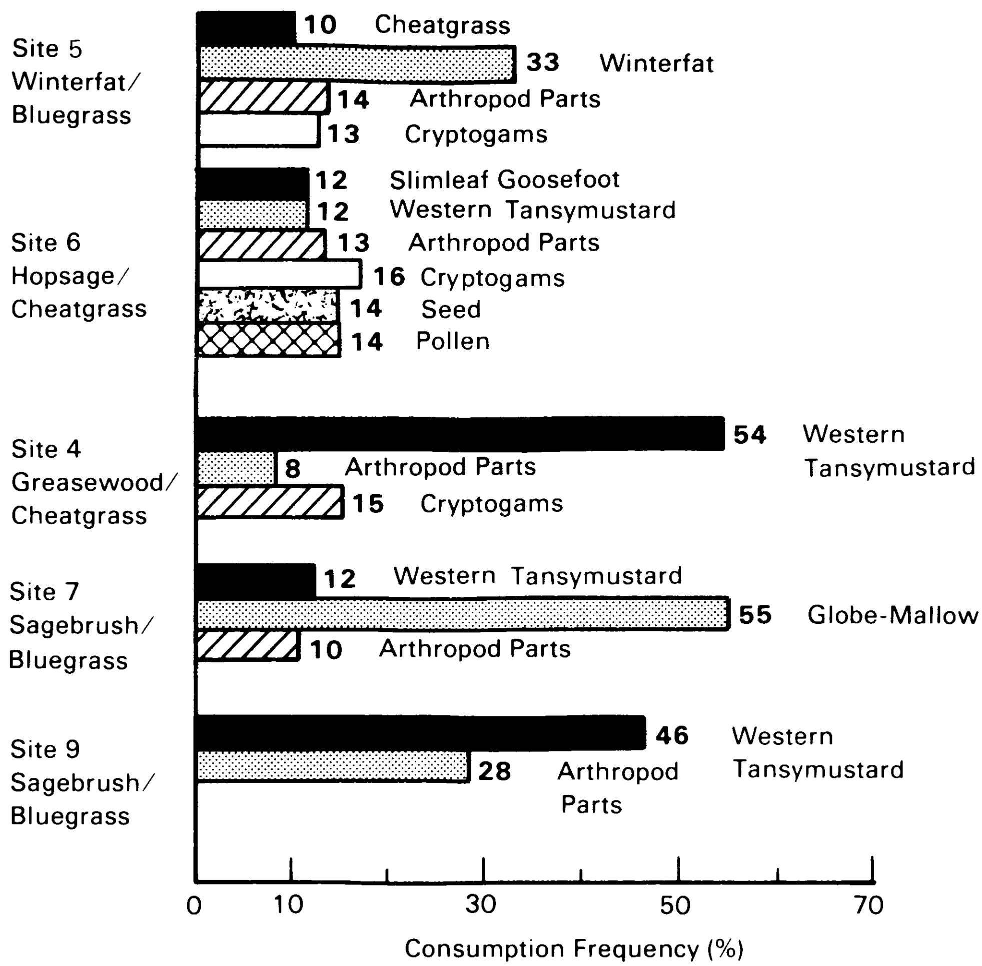

Fig. 3. Consumption frequency (%) of major plant species by *E. hispilabris.*

bluegrass community (Site 7) during this study, and this analysis reflects only those food items available in that community (Table 2). Although diet for this species included 16 food items, only three had a high ingestion frequency: western tansymustard (37%), cheatgrass (14%), and big sagebrush (14%).

Eleodes granulata LeConte. Twenty-four food items were consumed by this species (Table 2). Major food items were cryptogams (23%), cheatgrass (18%), western tansymustard (15%), and winterfat (11%). All others comprised 7% or less of the diet. Consumption frequency for the two sites where this species was abundant is shown in Figure 2.

Eleodes hispilabris Blaisdell. A total of 34 food items was consumed by this species (Table 2). Forbs were the most important category of food plants; only western tansymustard (18%) and globe-mallow (17%) were abundant in their diet. The many different food items consumed (mostly at low frequencies) and the shift in food items taken from different study sites (Fig. 3) indicate that *E. hispilabris* is an omnivorous feeder.

Eleodes humeralis LeConte. There were 10 food items in the diet of *E. humeralis*, all but two of them incidental (Table 2). In the greasewood community (Site 4), big sagebrush (51%) and rabbitbrush (36%) were the most important plant species in the diet. This supports field observations that *E. humeralis* occurs in abundance only in shrub-dominated areas (Sheldon & Rogers 1984). *E. humeralis* is obviously a stenophage.

Eleodes nigrina Blaisdell. Twenty-two food items were consumed by this species (Table 2). Most frequently consumed were winterfat (16%), western tansymustard (15%), and big sagebrush (12%). Grasses were an insignificant part of the diet.

Populations inhabiting specific communities seemed to adjust their feeding to available plant species (Fig. 4). In the winterfat community (Site 5), this beetle concentrated on winterfat and arthropod parts but took little sagebrush or western tansymustard. In the greasewood community (Site 4), greasewood was the most frequently consumed shrub, although sagebrush was also eaten. Both western tansymustard and cryptogams were also frequently ingested. Beetles in the sagebrush–blue-

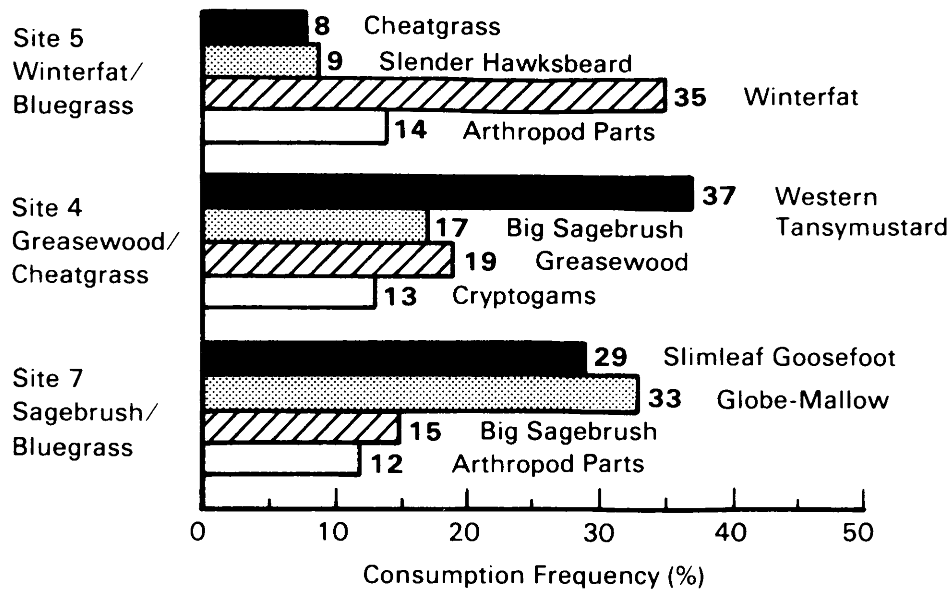

Fig. 4. Consumption frequency (%) of major plant species by *E. nigrina*.

grass community (Site 7) selected sagebrush, globe-mallow, goosefoot, and arthropod parts.

Eleodes novoverrucula Boddy. This darkling beetle consumed 21 different food items (Table 2), preferring cryptogams (30%) and big sagebrush (16%). None of the other ingested food plants comprised more than 9% of the total diet.

There was a high ingestion frequency of sagebrush in the greasewood (Site 4), and winterfat (Site 5) communities, but a low one in the hopsage (Site 6) community, where cryptogams, hopsage, and Russian thistle were the major food items (Fig. 5).

Eleodes obscura Say. Fourteen food items were found in the diet of this species (Table 2). Russian thistle (26%), cheatgrass (24%), and slender hawksbeard (17%) were the major plants in the diet. This beetle is not abundant, and only 13 individuals are included in this diet analysis; therefore, dietary preferences observed here may not be representative of the population as a whole.

Eusattus muricatus LeConte. Twenty-one food items occurred in the diet of *E. muricatus* (Table 2), which appears to be restricted to sandy habitats. Samples were collected only from Site 8. Western

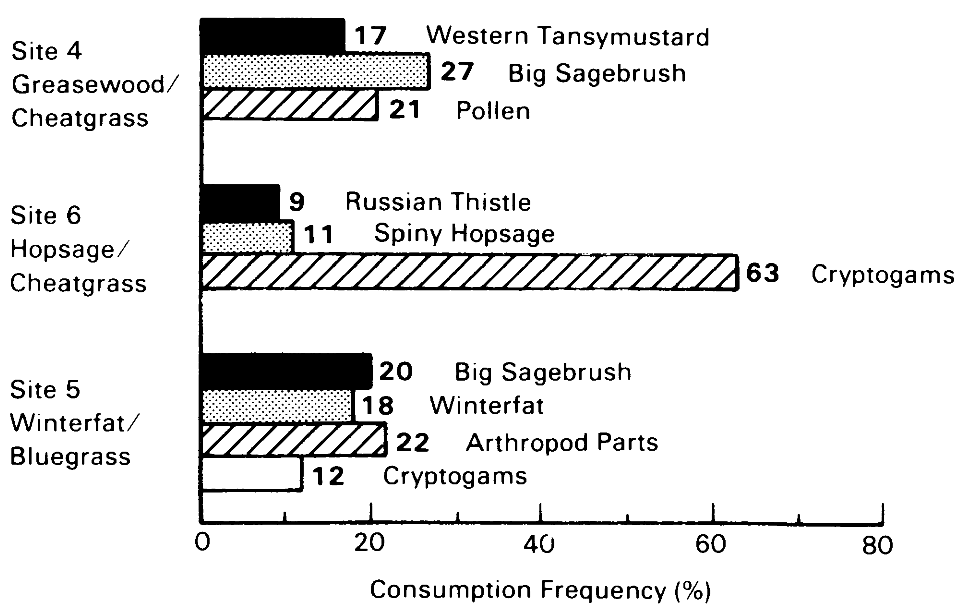

Fig. 5. Consumption frequency (%) of major plant species by *E. novoverrucula*.

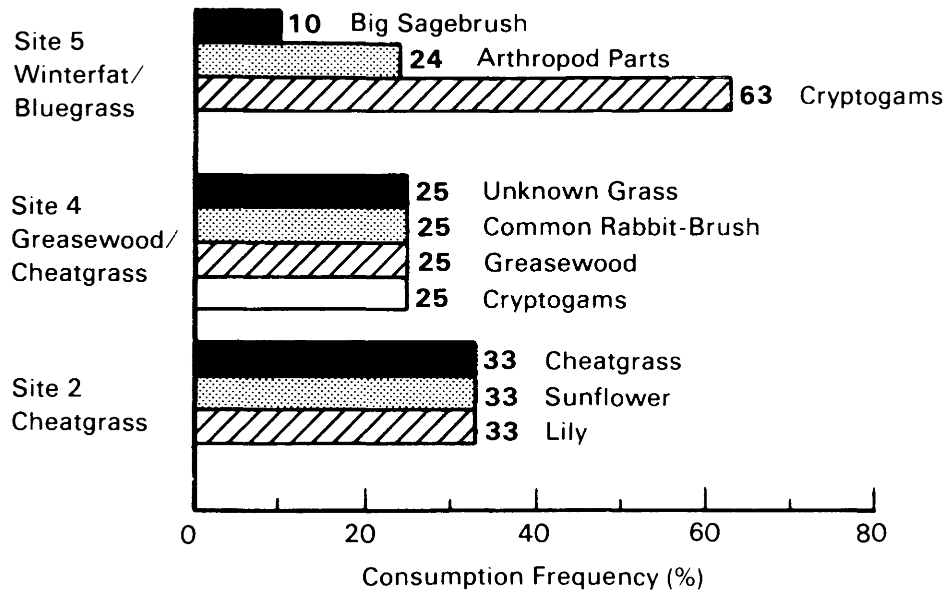

Fig. 6. Consumption frequency (%) of major plant species by *O. hispidula*.

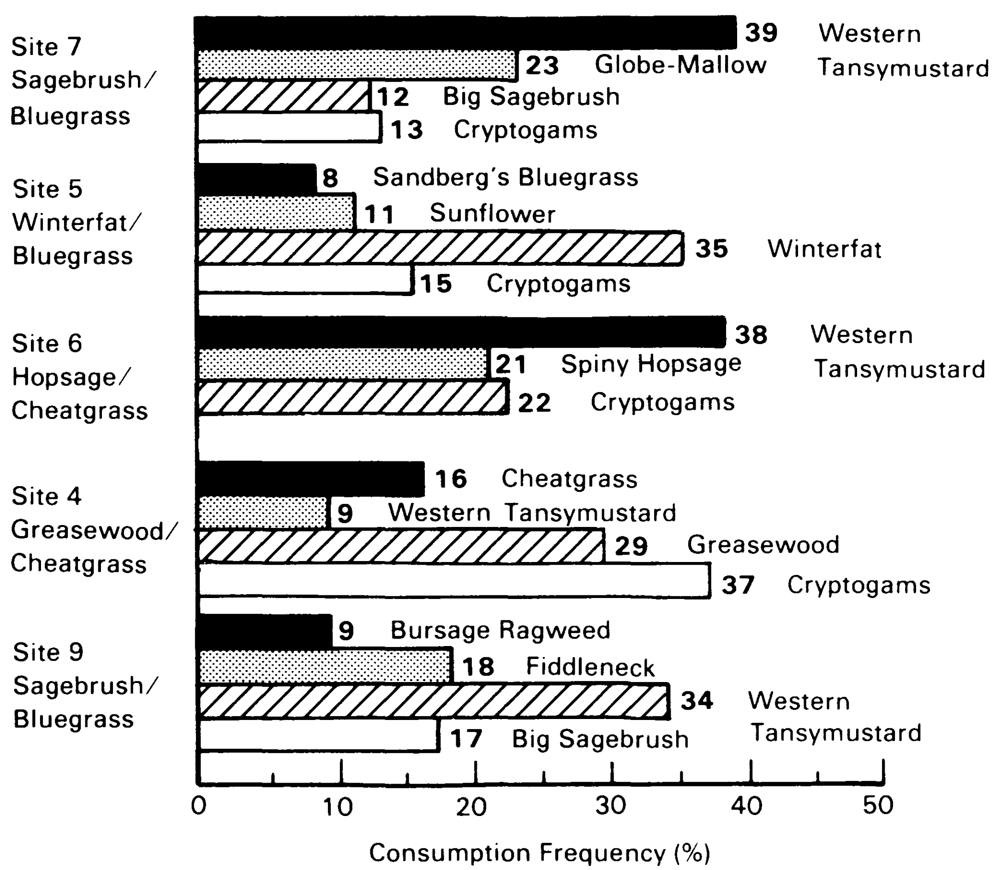

Fig. 7. Consumption frequency (%) of major plant species by *P. densicollis*.

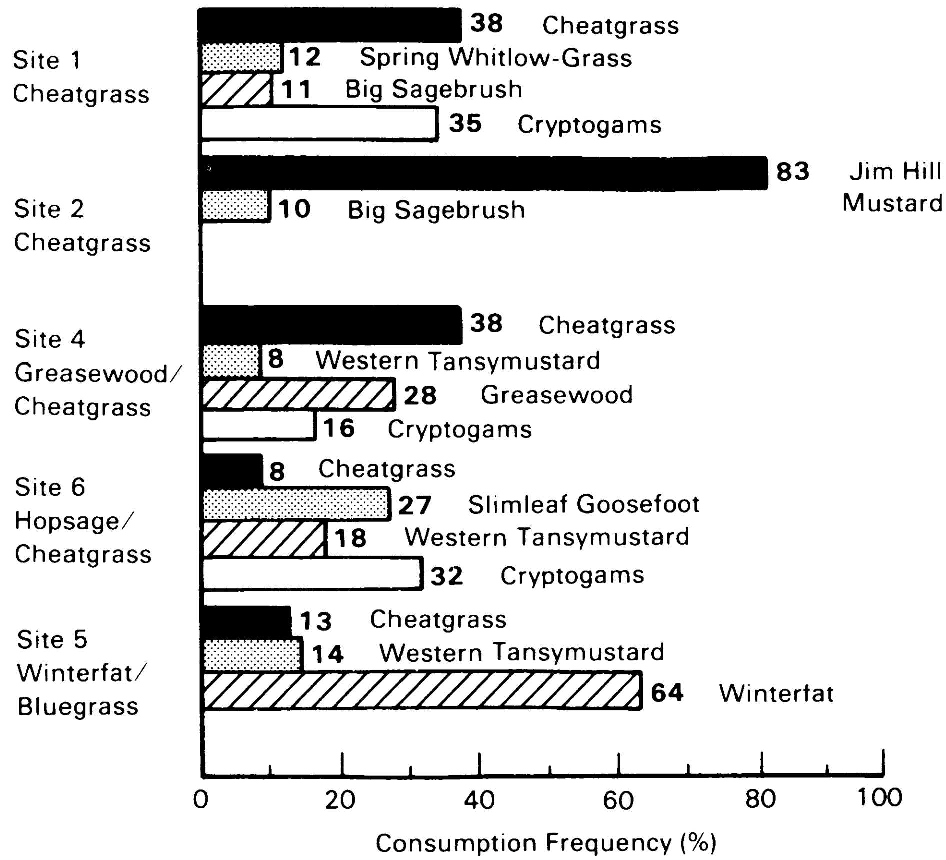

Fig. 8. Consumption frequency (%) of major plant species by *S. puncticollis*.

tansymustard (22%) and big sagebrush (50%) were the only species consumed in large proportions. All other food items occurred in the diets with less than 3% frequency.

Oxygonodera hispidula Horn. This beetle consumed 11 different food items (Table 2). Only three—cryptogams (46%), arthropod parts (19%), and big sagebrush (11%)—occurred with a high frequency across the sites where it was abundant (Table 2, Fig. 6).

Philolithus densicollis Horn. A total of 36 different food items was consumed by this species, the most recorded for any species in this study. Western tansymustard (17%), cryptogams (17%), winterfat (12%), big sagebrush (9%), and greasewood (7%) were the most frequently consumed food items across sites (Table 2). This beetle is clearly an omnivorous feeder, but it tended to select western tansymustard, sagebrush, and cryptogams consistently. Cryptogams are an important diet component at nearly all study sites (Fig. 7).

Stenomorpha puncticollis LeConte. Twenty-three food items were selected by this species (Table 2). Food items of importance include cheatgrass (23%), Jim Hill mustard (16%), winterfat (14%), cryptogams (13%), and greasewood (11%). Cheatgrass was consumed at most study sites where this beetle was collected (Figure 8). The lack of cheatgrass consumption in the lower old field (Site 2) is associated with a high frequency of ingestion for Jim Hill mustard, the latter probably being preferred.

Discussion

Measurement of dietary niche overlap permits grouping of beetle cohorts with similar feeding patterns. *Blapstinus* spp. are not included in this analysis because specific determinations were not made between *B. substriatis* and *B. discolor*.

A dendrogram was constructed from dietary niche overlap data to show the relation between food habits (Fig. 9). The unweighted paired-group method of clustering resulted in the highest cophenetic correlation, a measure of agreement between the dendrogram and the initial measures of interobject distance; i.e., niche overlap (Hartigan 1975).

The diet of *Eleodes obscura* was distinct from those of the other beetles in containing only annual plant (weedy) species. All the other beetles contained perennial plants to varying degrees. *E. humeralis* and *Eusattus muricatus* formed a group

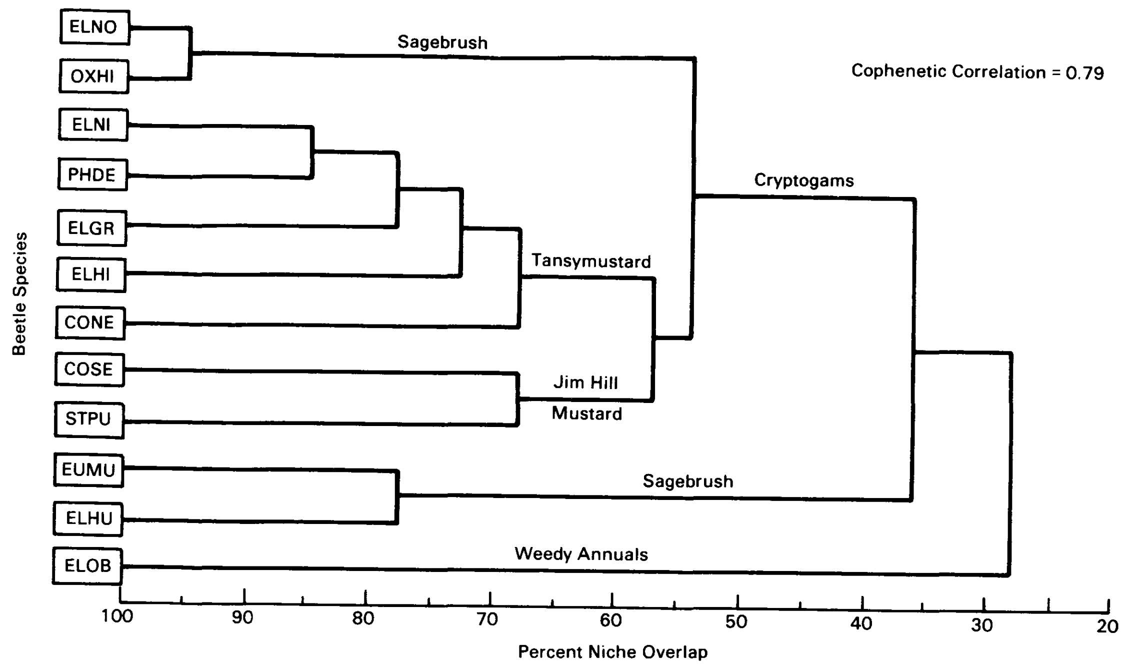

Fig. 9. Dendrogram constructed from dietary niche overlap data to show food habit relationships amidst beetle species. See footnote Table 2, for abbreviations of beetle names.

whose diet was >50% sagebrush but lacked any cryptogams.

The remaining beetles are joined because cryptogams were a significant component of their diets. *E. novoverrucula* and *Oxygonodera hispidula* formed a subgroup whose diets consisted primarily of cryptogams and sagebrush. *Stenomorpha puncticollis* and *Coniontis setosa* formed another distinct subgroup characterized by a highly diverse diet with Jim Hill mustard a major component. The remaining beetles (*Conisattus rectus, Eleodes hispilabris, E. granulata, P. densicollis,* and *E. nigrina*) have a diverse diet with western tansymustard as a dominant component.

This study indicates that dietary distinctions are made by the tenebrioned beetles occupying our study sites. The underlying reasons for these distinctions are unknown but are probably related to temporal and spatial factors in addition to food preferences. Distributions of these beetles are related to soil texture, vegetation composition, and season (Sheldon & Rogers 1984). Partitioning of food resources may be acting to refine further the niches of these beetles.

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