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Patterns of vegetation and grasshopper community composition

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Summary. A study was conducted to evaluate differences in rangeland grasshopper communities over environmental gradients in Gallatin Valley, Montana, USA. The concept of habitat type (Daubenmire 1966) was used as a basis for discriminating between groupings of patches based on vegetation. A total of 39 patches were selected that represented five recognized grassland habitat types (Mueggler and Stewart 1980), as well as two disturbed types (replanting within a known habitat type). Repeated sampling in 1988 of both the insect and plant communities yielded a total of 40 grasshopper (19664 individuals) and 97 plant species. Detrended Correspondence Analysis (DCA) indicated that patch classifications based on presence and percent cover of plants were appropriate and showed good between-group (habitat type) separation for patches along gradients of precipitation/elevation and plant community complexity. Results from undisturbed habitats showed that plant and grasshopper species composition changed over observed environmental gradients and suggested that habitat type influenced not only species presence, but also relative abundance. Discussion is presented that relates results with patch-use and core and satellite species paradigms.

Key words: Patterns – Patch use – Grasshoppers – Communities – Habitat type

Ecologists have long recognized variation in plant and animal communities along environmental gradients such as elevation, moisture, and temperature. More recently, emphasis has been placed on identifying and explaining the ways in which environmental factors influence co-occurring species. Through the study of patches and patch dynamics, ecologists have been able to identify patterns and occasionally processes that are important to the understanding, conservation, and management of natural systems (Pickett and White 1985).

The grasslands of the Northern U.S. Rocky Mountains present wide variations in patch structure to important insect herbivores such as grasshoppers. Within the array of grass and shrub patches in western Montana (in aggregations called habitat types (h.ts.), Mueggler and Stewart 1980) available for exploitation by grasshoppers, several environmental gradients have been identified (Weaver 1979a, b). However, little work has been done on the structure of the grasshopper communities inhabiting the mosaic of habitats in this region (Anderson 1973).

A major question still facing ecologists involved with conservation and management is how grasshopper community composition varies in space. In this study, grasshoppers were selected as the representative and dominant herbivores and our main objective was to determine whether variation in grasshopper community structure existed along recognized grassland environmental gradients.

Methods

The study area was located in the northern part of Gallatin County, Montana, USA (longitudes 111°00′–111°40′ east-west, latitudes 46°00′–45°45′ north-south) in the *Agropyron spicatum* province of the western steppe region of the United States (Daubenmire 1978).

Defining patches and patch selection

Before any study of non-random patch use can be conducted, a scale must be selected. In this study, we first identified patches in the manner described by White and Pickett (1985) where the term patch refers to discrete spatial patterns, but size and internal homogeneity of patches is unconstrained. The White and Pickett (1985) definition also implies that there can be a relatedness between patches and to the surrounding matrix.

We used the method of "habitat typing" (Daubenmire 1952, 1959, 1966, 1970, and Daubenmire and Daubenmire 1968) to select patches in an effort to minimize vegetational differences between patches within a particular habitat and ensure that the habitats selected were discrete and distributed over known environmental gradients (Weaver 1979a, b; Taylor et al. 1984). Support for eco-

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logical differences among habitat types previously identified in Montana by Mueggler and Stewart (1980) can be found in 1) climate/vegetation associations (Weaver 1979a, b) and soil/habitat type (h.t.) associations (Munn et al. 1978).

Patch selection

Thirty-nine patches in five h.ts. (Mueggler and Stewart 1980) were selected for study (Table 1). Ten patches in either of two h.ts. which had been plowed and planted were selected to contrast native and replanted patches within the same h.t. (Table 1). Replanted patches were not recent disturbances and we, therefore, treated them as distinct types. The order of habitats in Table 1 represents a gradient of precipitation and elevation, with STCO/BOGR lower and drier, and FEID/AGSP higher and wetter (Mueggler and Stewart 1980).

Patches were selected in the spring (early May) and classified based on the presence of indicator vegetation (see Mueggler and Stewart 1980). The spring and early summer grasshopper species had yet to hatch, so patch selection was not biased with regard to the presence or absence of grasshoppers. These patch classifications were considered tentative until subsequent detailed vegetation sampling and analyses supported our determinations. We included only locations with light to moderate livestock (cattle, horses, etc.) grazing histories, because we wished to avoid this potentially confounding influence (Mueggler and Stewart 1980). The minimum size of any one patch was 10 ha and no two distinct native patches shared a common border. For comparisons between native and replanted patches within h.t., patches were always adjacent, but sampling was conducted only in representative type and not in the ecotones. Data on precipitation and elevation from each patch were obtained from Ross and Hunter (1976) and U.S. Geological Survey 7.5 minute quadrangle maps, respectively.

Vegetation sampling

The vegetation at each patch was sampled during July–August of 1988 to coincide with peak standing cover of plants. Thirty-five 1/10 m^2 (20 × 50 cm) quadrats were sampled along a randomly selected transect within each patch. In each quadrat, percent canopy cover of each plant species, litter, moss/lichen, and bare ground were estimated in 5% increments following the methods described by Daubenmire (1959) and those used in several studies for vegetation classification (Pfister et al. 1977; Harvey and Weaver 1979; Mueggler and Stewart 1980). Subsequent analyses were based on mean cover-estimates of plant species over all quadrats at a patch. Plant species that were unidentifiable in the field were collected and returned to the laboratory for identification.

Table 1. Habitat types (Mueggler and Stewart (1980)) sampled for grasshoppers in Gallatin Valley, Montana, USA, 1988

Habitat type code	Predominant plant species	Number of plants sampled
STCO/BOGR	*Stipa comata/* *Bouteloua gracilis*	8
Agcr/Mesa[a]	*Agropyron cristatum/* *Medicago sativa*	6
AGSP/BOGR	*A. spicatum/B. gracilis*	5
AGSP/POSA-STCO	*A. spicatum/* *Poa sandbergii,* *S. comata* phase	4
ARAR/AGSP	*Artemisia arbuscula/* *A. spicatum*	5
FEID/AGSP	*Festuca idahoensis/* *A. spicatum*	7
Brin/Mesa[b]	*Bromus inermis/* *M. sativa*	4

[a] Replanted patches on STCO/BOGR habitats

[b] Replanted patches on FEID/AGSP habitats

Detrended Correspondence Analysis (DCA) was selected for the analysis of within and between h.t. similarities in vegetation (Hill 1979; Hill and Gauch 1980; Kent and Ballard 1988). DCA is an ordination technique, similar to principal component analysis, for multivariate data and is designed to summarize species-sample data (species-patch data in our case). Resulting DCA plots in two or three dimensions are useful in that increasing distance between patches reflects decreasing similarity with respect to vegetation.

Other data, for example, on the number of plant species and percent grasses, etc. were first evaluated with an omnibus Kruskal-Wallis non parametric one-way analysis of variance (Siegel 1956) to test the null hypothesis of no differences in the measured variable across habitats. If the result of the Kruskal-Wallis test was significant ($\alpha = 0.05$), orthogonal comparisons were made using the non parametric Mann-Whitney *U*-test (two-tailed, $\alpha = 0.05$, Siegel 1956).

Herbivore sampling – grasshoppers

Sweep net collections were made at each patch, in the same area as the vegetation transects, three times (late May/early June, late July, late August) during 1988. Two hundred sweeps per patch were collected at each sampling period between 0930 and 1600 h under sunny skies (<15% cloud cover), and light winds (<25 km h^{-1}). Each sweep consisted of traversing an arc of 180° through the vegetation with a net, as described by Evans (1984, 1988).

Grasshoppers were collected at three times to insure detection of species with different phenological patterns; some species overwinter as eggs and emerge in the spring, while others spend the summer months as eggs and overwinter as nymphs. Previous studies of grasshoppers in tallgrass prairie found that in comparison with night trapping, sweep samples provided good estimates of relative abundance and species composition (Evans et al. 1983; Evans 1988). Therefore, sweep sampling was suitable for discriminating potential differences in grasshopper species composition and relative abundance (from pooled samples comprised of 600 sweeps) across the selected h.ts.

DCA was used, as in the vegetation analyses, to evaluate similarities between grasshopper communities among the h.ts. sampled. Also, other analyses (i.e., species richness, percent abundance, etc.) were conducted with non parametric statistical tests in the same order and manner as described above for vegetation. The Fisher Exact Probability Test (two-tailed, $\alpha = 0.05$, Siegel 1956) was used as an additional comparison of whether individual grasshopper species were collected differentially in contrasting h.ts.

Results

Vegetation patterns

A DCA on the percent cover by plant species (total of 97), and patch demonstrated that our *a priori* h.t. classifications (Mueggler and Stewart 1980) were appropriate and illustrated the relatedness of patches within h.t. Groupings of patches (i.e., h.t.) were apparent along a cline based on plant species composition and percent cover (Fig. 1). For example, scores generated by the

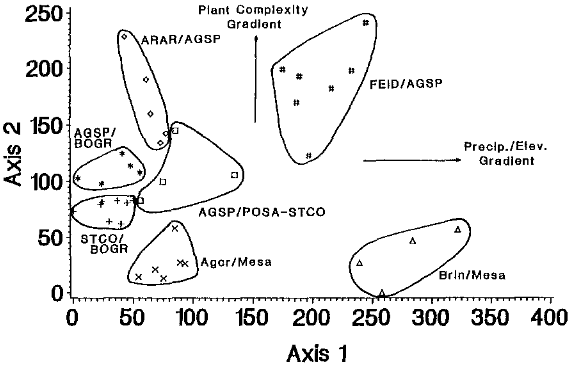

Fig. 1. Detrended Correspondence Analysis of plant community composition for 39 patches representing a range of habitat types in Gallatin Valley, Montana, USA, 1988. Eigenvalues for x and y axes are 0.60 and 0.27, respectively. Habitat codes as in Table 1

DCA for axis 1 appeared to represent a gradient of increasing precipitation/elevation as evidenced by the relationship of ordination scores (axis 1) and these variables. Positions of the two replanted h.ts. (Fig. 1) with Agcr/Mesa at the lower and drier end of the gradient and Brin/Mesa at the higher and wetter end (see also Fig. 2) also supported this interpretation. Eighty-seven percent of the variance in the data was explained by the two axes (60 percent in the first axis alone, Fig. 1). Spearman rank correlations (r_s, Siegel 1956) showed that plant community DCA axis 1 scores were correlated with precipitation and elevation (Table 2). Correlations computed, but not listed in Table 2, between plant community DCA axis 1 scores and the proportion of species represented by grasses or forbs, and total number of plant species were not significant ($P > 0.05$).

The scores of the DCA for axis 2 (Fig. 1) appeared to be associated with a plant community complexity gradient. Axis 2 scores, for the DCA on plant communities, were positively correlated with the proportion of plant species represented by forbs and were negatively correlated with the proportion of plant species represented by grasses (Table 2). Axis 2 scores were also positively correlated with the total number of plant species (Table 2). However, change in life form, dominance of species, or uniqueness of species to particular h.ts. across the DCA axis 2 also contributed to community complexity. Among the native h.ts., differences between STCO/BOGR and AGSP/BOGR patches were related to increases in *A. spicatum* dominance, species richness (Fig. 3a), and percent grass species present (Fig. 3b). Although the number of plant species as well as percent grasses were similar among the AGSP/BOGR, ARAR/AGSP, and FEID/AGSP patches (Fig. 3), the separation of h.ts. that resulted from the DCA was related to 1) the increases in prevalence of shrub species such as *Artemisia arbuscula* and 2) associated forbs in the ARAR/AGSP patches and the grass *Festuca idahoensis*, the forb *Balsamorhiza sagittata*, and other associated forbs in the FEID/AGSP patches. The AGSP/POSA-STCO h.t. represented an intermediate type and patches showed less aggregation. This was probably related to the highly variable precipitation levels among patches in this h.t. (Fig. 2a), as well as the extreme slopes associated with this typal community.

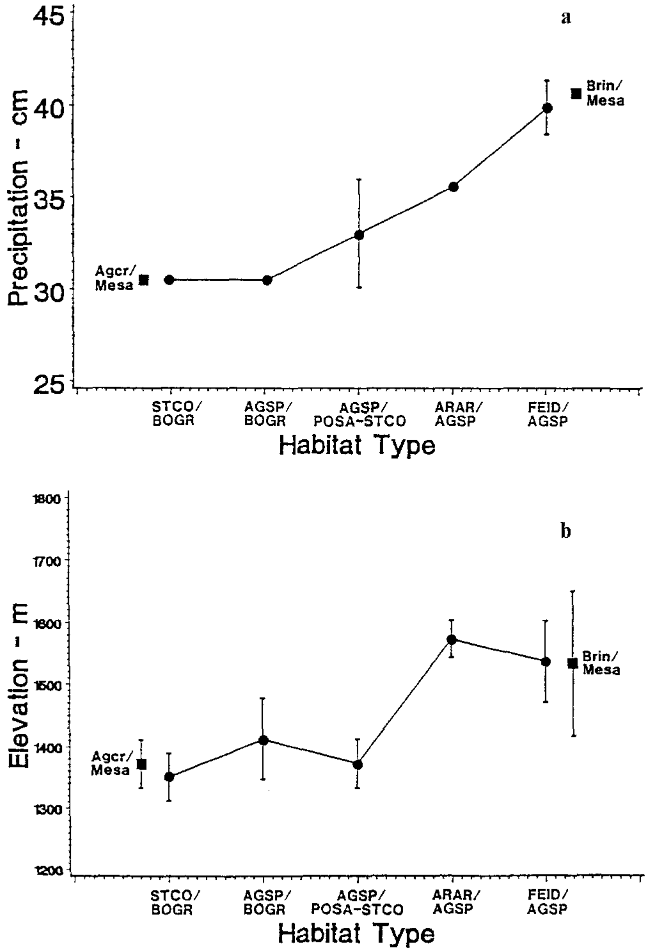

Fig. 2a, b. Precipitation (**a**) and elevation (**b**) mean values ($\pm 2 \cdot$SE) for a range of habitat types surveyed for grasshoppers and vegetation in Gallatin Valley, Montana, USA, 1988. Habitat codes as in Table 1

Grasshopper patterns – local abundance and rarity

A total of 40 grasshopper species (19664 individuals, nymphs and adults) were collected from the seven h.ts. during the 1988 field season (Table 3). At the scale of the entire valley, all patches combined, average local abundance of individual species was positively correlated with the number of patches occupied (Fig. 4a). A notable exception to this was *Stenobothrus brunneus* that was locally abundant at only one patch within the ARAR/AGSP h.t. (Table 3). The distribution of species occurrence was skewed left with 13 species (33%) collected at four or fewer of the possible 39 patches (Fig. 4b). Alternatively, only two species (5%) were collected at 35 or more patches.

Associations with habitat type

The mean number of grasshopper species by subfamily (Table 3) within h.t. showed several significant differ-

Table 2. Selected correlations computed for comparisons between DCA axes scores and environmental variables

Correlations	r_s[a]	P
Plant communities DCA –		
Axis 1 scores vs. precipitation	0.75	<0.001
vs. elevation	0.53	<0.001
Axis 2 scores vs. precipitation	0.43	<0.01
vs. elevation	0.51	<0.002
vs. proportion of plant species represented by grasses	−0.37	<0.05
vs. proportion of plant species represented by forbs	0.37	<0.05
vs. total number of plant species	0.80	<0.001
Axis 2 scores vs. axis 1 scores	0.09	>0.05
Grasshopper communities DCA –		
Axis 1 scores vs. precipitation	0.69	<0.001
vs. elevation	0.48	<0.005
Axis 2 scores vs. precipitation	0.28	>0.05
vs. elevation	0.21	>0.05
vs. proportion of plant species represented by grasses	−0.35	<0.05
vs. proportion of plant species represented by forbs	0.30	$0.05<P<0.10$
vs. total number of plant species	0.38	<0.05
Axis 2 scores vs. Axis 1 scores	−0.01	>0.05
Comparisons between grasshopper and plant communities DCA runs –		
Grasshopper DCA axis 1 scores vs. plant DCA axis 1 scores	0.65	<0.001
vs. plant DCA axis 2 scores	0.15	>0.05
Grasshopper DCA axis 2 scores vs. plant DCA axis 1 scores	−0.09	>0.05
vs. plant DCA axis 2 scores	0.33	<0.05

[a] Spearman rank correlation (Siegel 1956)

ences (Table 4). In the arid, but more floristically complex AGSP/POSA-STCO patches (Figs. 1, 3), there were significantly more Catantopinae and Gomphocerinae species present when contrasted with the number of Oedipodinae species. The more mesic patches within the native FEID/AGSP and replanted Brin/Mesa h.ts. (Figs. 1, 3) were dominated by Catantopinae species (Table 4). Contrasts of species numbers between native and replanted h.ts., Agcr/Mesa-STCO/BOGR and Brin/Mesa-FEID/AGSP (Table 4), showed no significant differences at either end of the precipitation/elevation gradient. However, within subfamily contrasts between the most arid h.t. (STCO/BOGR) and the most mesic h.t. (FEID/AGSP) showed significant increases, going from arid to mesic, in the number of Catantopinae species and a corresponding reduction in the numbers of Gomphocerinae and Oedipodinae species ($P<0.05$).

Distribution along gradients – axis 1

Grasshopper communities appeared to be sensitive to the same gradients identified for plants. Axis 1 scores for the DCA on grasshopper communities were correlated with both precipitation and elevation as well as with the axis 1 scores for the DCA on plant communities (Table 2). Correlations computed between grasshopper community axis 1 DCA scores and the proportion of plant species represented by forbs and grasses as well as with the total number of plant species were not significant ($P>0.05$).

Contrasts of grasshopper community composition at the species level at either end of the precipitation/elevation gradient show three general groups (Table 5). In the first group, species like *Phlibostroma quadrimaculatum* and *Xanthippus corallipes* were found only in patches associated with the arid STCO/BOGR h.t. (Group 1, Table 5). Other species such as *Aulocara elliotti*, *Ageneotettix deorum*, and *Psoloessa delicatula* (Group 1, Table 5), though collected at both ends of the gradient, were present at a much higher percent of the drier STCO/BOGR patches and constituted a much greater percent of the population at those patches than at patches within the FEID/AGSP h.t. Alternatively, there were grasshopper species that showed affinities for the mesic FEID/AGSP patches. For example, *M. dawsoni* was found only in the FEID/AGSP patches (when contrasting STCO/BOGR and FEID/AGSP h.ts.) and species such as *Phoetaliotes nebrascensis* and *M. bivittatus* (Group 3, Table 5), while present at both ends of the gradient, were much more common in the mesic FEID/AGSP patches.

In the second group, there were a number of grasshopper species that were present at most patches within habitats at either end of the gradient (Group 2, Table 5). Species like *Amphitornus coloradus* and *M. sanguinipes*, while present at a high percentage of patches within h.ts. at either end of the precipitation/elevation gradient (Table 3), also constituted a significant portion of the resident populations (Table 5). Alternatively, *M. packardii* and *Arphia pseudonietana*, while present in both native h.ts. (Table 3), generally made up a small percentage

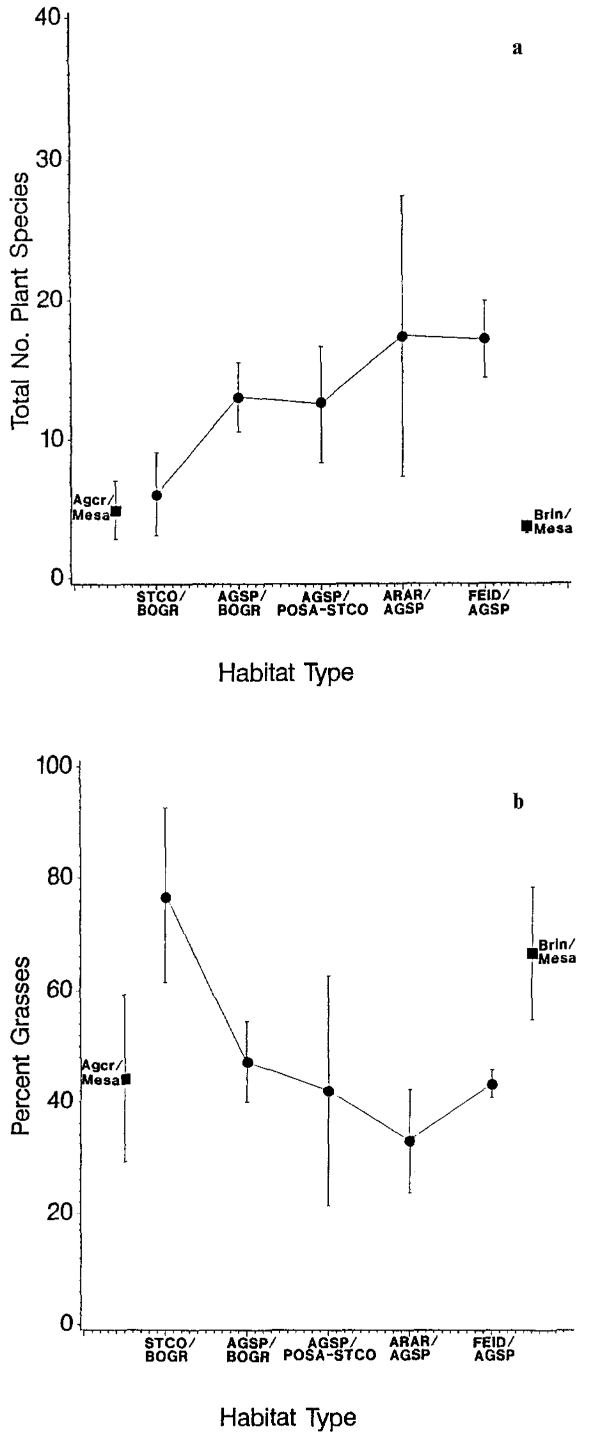

Fig. 3a, b. Total number of plant species (**a**) and percent grass species (**b**) mean values (± 2·SE) for a range of habitat types surveyed for grasshoppers and vegetation in Gallatin Valley, Montana, USA, 1988. Habitat codes as in Table 1

of the resident populations (Table 5). Two species, *M. infantilis* and *Aeropedellus clavatus*, appeared to be transition species at the dry and wet ends of the precipitation/elevation gradient (Table 5), respectively. Although both species differed significantly in relative abundance at extremes of the gradient, they did not differ in frequency of patches occupied in the contrasting h.ts.

Distribution along gradients – axis 2

Grasshopper communities also appeared to be influenced by plant community complexity. Axis 2 scores for the DCA on grasshopper communities showed a negative correlation with the proportion of plant species represented by grasses and positive correlations with the total number of plant species and with the axis 2 scores for the DCA on plant communities (Table 2).

Contrasts made between grasshopper species present from the STCO/BOGR patches with those from the dry, but more floristically complex ARAR/AGSP patches (Fig. 1) also showed interesting results. Grasshopper species such as *Circotettix undulatus*, *S. brunneus*, *Cratypedes neglectus*, *Hadrotettix trifasciatus* and *M. dawsoni* were found in the ARAR/AGSP patches, but not in the STCO/BOGR patches (Table 3). *Trimerotropis campestris*, while collected at either end of the gradient, was significantly (Fisher Exact Probability Test, Mann-Whitney *U*-test) more common in the ARAR/AGSP patches. Alternatively, species such as *Trachyrhachys kiowa*, *P. quadrimaculatum*, and *A. coloradus*, were significantly (Mann-Whitney *U*-test) more common, when present, in the STCO/BOGR patches when compared to grasshopper communities in the ARAR/AGSP patches, but did not show significant differences in the frequency of collection (Fisher Exact Probability Test) and association with the two h.ts. considered along this gradient ($P < 0.05$).

The DCA for all grasshopper species in all h.ts., based upon presence and relative abundance, revealed trends similar to those found in Table 5. For the sake of clarity only 25 of the 40 species analysed are presented in Fig. 5. Within a DCA, species that fail to show any affinity to either end of a range of samples (h.ts. in this case), will occupy central portions of the axes (Fig. 5). The grasshopper species in Group 2, Table 5 tended to cluster in the central portion of the DCA axis 1 (Fig. 5). Grasshopper species associated with arid (Group 1, Table 5) and mesic (Group 3, Table 5) h.ts. clustered to the left and right of DCA axis 1, respectively (Fig. 5). Additionally, species unique to the ARAR/AGSP patches were found at the upper end of the DCA axis 2 (Group 4, Fig. 5, Table 3).

It is important to note that these DCA results (Fig. 5) come from the analysis of grasshopper communities over all 39 patches rather than patches from habitats at either end of the precipitation elevation gradient (Table 5). When all grasshopper communities are considered, the transition species *M. infantilis* (Table 5) appears to be more closely related to Group 1 species (Fig. 5, Table 5). *A. clavatus* appears to be clearly related to the Group 2 species (Fig. 5, Table 5).

Discussion

Grasshopper/vegetation patterns

Grasshopper species showed non-random use patterns across the range of patches sampled in Gallatin Valley,

Table 3. Grasshopper (Orthoptera: Acrididae) presence (+) or absence (−) by subfamily and species for each habitat type. Gallatin Valley, Montana, USA, 1988

	Habitat type						
	Agcr/ Mesa	STCO/ BOGR	AGSP/ BOGR	AGSP/ POSA-STCO	ARAR/ AGSP	FEID/ AGSP	Brin/ Mesa
Catantopinae							
Acrolophitus hirtipes	−	+	+	+	+	+	−
Encoptolophus costalis	+	+	−	+	+	+	+
Hesperotettix viridis	+	−	+	+	+	+	−
Melanoplus bivittatus	+	+	+	+	−	+	+
Melanoplus bruneri	−	−	−	−	−	−	+
Melanoplus confusus	+	+	+	+	+	+	+
Melanoplus dawsoni	−	−	+	+	+	+	+
Melanoplus femurrubrum	−	+	+	+	+	+	+
Melanoplus gladstoni	+	+	+	+	+	+	−
Melanoplus infantilis	+	+	+	+	+	+	+
Melanoplus keeleri	−	−	+	−	−	+	−
Melanoplus occidentalis	−	+	−	−	−	−	−
Melanoplus oregonensis	−	−	−	−	−	+	+
Melanoplus packardii	+	+	+	+	+	+	−
Melanoplus sanguinipes	+	+	+	+	+	+	+
Phoetaliotes nebrascensis	−	+	+	+	+	+	+
Oedipodinae							
Arphia conspersa	+	+	+	+	+	+	+
Arphia pseudonietana	+	+	+	+	+	+	+
Camnula pellucida	+	+	+	−	+	+	+
Circotettix carlinianus	−	−	+	−	−	−	−
Circotettix undulatus	−	−	−	−	+	−	−
Cratypedes neglectus	+	−	−	−	+	−	−
Dissosteira carolina	+	+	−	−	−	+	−
Hadrotettix trifasciatus	−	−	−	−	+	−	−
Metator pardalinus	+	+	+	+	+	+	−
Spharagemon campestris	+	+	+	+	+	−	−
Spharagemon collare	−	−	+	−	−	−	−
Spharagemon equale	+	+	+	+	+	−	−
Trachyrhachys kiowa	+	+	+	+	+	+	−
Trimerotropis gracilis	+	−	−	−	−	−	−
Xanthippus corallipes	+	+	+	+	+	−	+
Gomphocerinae							
Aeropedellus clavatus	+	+	+	+	+	+	+
Ageneotettix deorum	+	+	+	+	+	+	−
Amphitornus coloradus	+	+	+	+	+	+	−
Aulocara elliotti	+	+	+	+	+	+	+
Chloealtis conspersa	−	−	−	−	−	+	−
Chorthippus curtipennis	−	−	−	−	−	+	+
Phlibostroma quadrimaculatum	+	+	+	+	+	−	−
Psoloessa delicatula	+	+	+	+	+	+	+
Stenobothrus brunneus	−	−	−	−	+	−	−

Montana. Although plant and grasshopper community compositions show variation among patches within h.t., obvious trends are apparent when contrasting the grasshopper communities between h.ts. at either end of the two gradients. Precipitation/elevation and plant community complexity gradients are important in separating patches into h.ts. and appear also to be important in structuring grasshopper community composition (Figs. 1 and 5, Tables 2–5). Although we did not design this study to show whether grasshopper communities are influenced directly by environmental factors or indirectly by differences in vegetation that affect such characteristics as microhabitat (Isely 1937; Joern 1982), oviposition patches (Kemp and Sanchez 1987), preferred food abundance (Joern 1979, 1983, 1985; Mulkern 1967; Mulkern et al. 1969), and predator escape (Wiens 1985), it is likely that the communities are shaped by both direct and indirect factors (Wiens 1985; Schoener 1986; Kingsolver 1989). Regardless of the specific factors shaping communities of rangeland grasshoppers, both between patch within h.t. and between h.ts., our results suggest that it is reasonable to expect certain grasshopper species will be present, given information on the resource production capabilities of a patch, as expressed

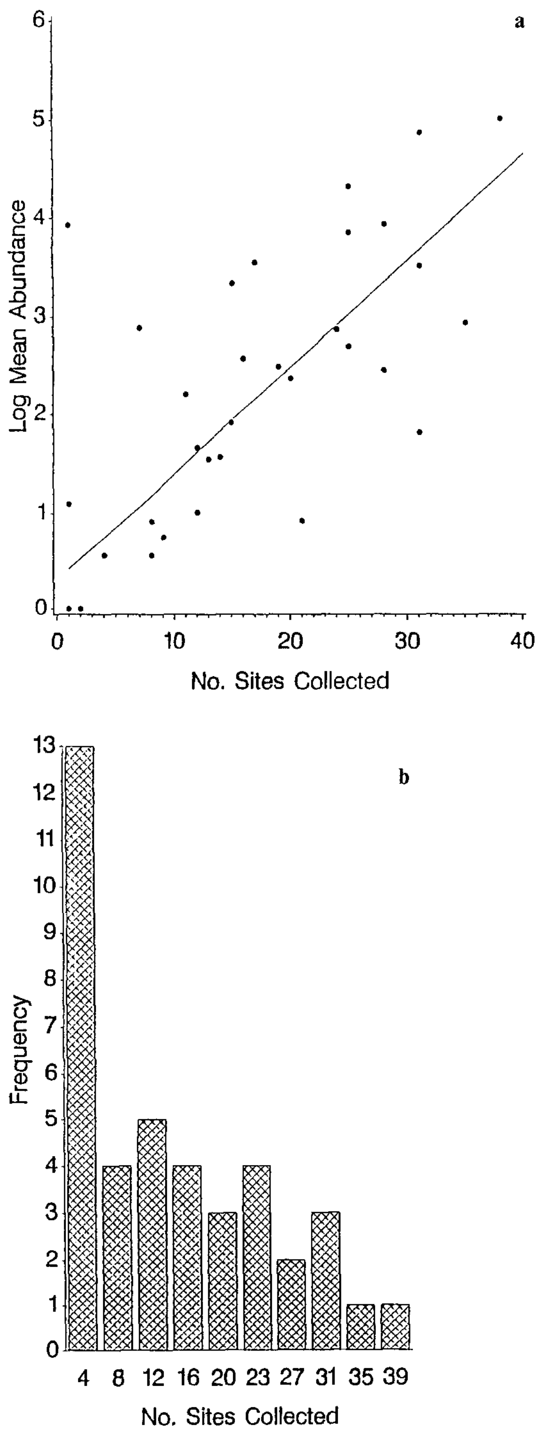

Fig. 4. (**a**) Relationship between ln (mean density) and the number of patches occupied and (**b**) distribution of frequencies of occurrence [$r^2=0.59$, $F=57.95$, $N=40$, $P=0.0001$] for 40 grasshopper species surveyed at 39 sites in Gallatin Valley, Montana, 1988

by h.t. This has important implications in conservation biology and insect management.

Core vs. satellite species

An important question for ecologists to address is that of how species aggregations vary in space (for reviews see Pickett and White 1985; Wiens 1976, 1985), because this has obvious implications for population persistence and stability. In an effort to classify species into discrete groupings, Hanski (1982) proposed the "core" and "satellite" species concept. In this model, Hanski argued that core species generally exhibit high local abundance and correspondingly high frequency in patches distributed regionally. Alternatively, satellite species with low local abundance were regionally infrequent.

For the grasshopper species that we studied, there appeared to be a general relationship between local grasshopper abundance and regional, valley-wide, frequency (Fig. 4a). As mentioned previously, the only clear exception to this was *S. brunneus* which was locally abundant at the only patch where it occurred. However, in spite of the relationship between local abundance and regional frequency, we did not find the bimodality in grasshopper species frequency distribution that would be expected from the Hanski (1982) model (Fig. 4b).

Our results suggest that, at least in terms of the 40 species found to inhabit Gallatin Valley, Montana, about 33% of the species that we encountered could be clearly classified as satellite species (Hanski 1982) (Fig. 4b). However, only two our about 5% of the species, *A. clavatus* and *M. sanguinipes*, could be considered true core species (Hanski 1982), because these species were collected at more than 90% of the patches monitored. The remaining 62% of the grasshopper species, though not found at all patches, were frequently found in one or more patches within h.ts. that were at either end of precipitation/elevation gradient (Tables 3, 5). Our results suggest that grasshoppers have a rather large group of intermediate species and that shifts in relative abundance, and therefore dominance, are influenced significantly by differences associated with h.t. (Table 5, Fig. 5). We did not see the clear dichotomy between core and satellite species that Hanski (1982) found in distributions of insects and plants. The large intermediate group found among grasshoppers collected over the range of h.ts. in this study may be related to den Boer's theory of "spreading of risk" (Den Boer 1968, 1981) where species distributed in many subpopulations over patches in a heterogenous landscape are likely to be more persistent.

On patches and gradients

It has been argued that it is naive to presume that nature is homogenous at any scale and that the operational difficulties of detecting and describing patches are significant (Wiens 1981, 1985). In this study, we found that the method of habitat typing was very useful in delimiting a range of vegetational conditions that represent discrete groupings of patches along the recognized environmental gradients of the Gallatin Valley (Fig. 1). Groups of patches within h.t., classified as being either more arid or mesic, were easily distinguished. Further, contrasts between the floristically simple (replanted) Agcr/Mesa and Brin/Mesa patches and the more complex types ARAR/AGSP and FEID/AGSP patches, respectively, were also clear. The variation found within the

Table 4. Mean number and SE ( ) of species by grasshopper (Orthoptera: Acrididae) subfamily and habitat type. Gallatin Valley, Montana, USA, 1988

	Habitat type						
	Agcr/Mesa	STCO/BOGR	AGSP/BOGR	AGSP/POSA-STCO	ARAR/AGSP	FEID/AGSP	Brin/Mesa
Catantopinae	4.2 (0.60)	4.8 (0.45)	6.4 (0.40)	7.0 a[a] (0.71)	4.0 (0.89)	7.0 bd (0.69)	6.3 ce (0.75)
Oedipodinae	6.0 (0.68)	4.6 (0.42)	5.6 (0.75)	3.3 af (0.48)	5.0 (1.05)	2.3 b (0.36)	2.3 c (0.48)
Gomphocerinae	5.0 (0.63)	5.6 (0.18)	5.8 (0.20)	5.3 f (0.48)	4.4 (0.60)	3.0 d (0.49)	2.0 e (0.41)

[a] Like letters indicate significant differences between subfamilies within h.t.

Table 5. For each commonly collected grasshopper species, percent of patches within habitat type in which it was present and mean percent of total grasshoppers collected by patch within habitat type ( ), Gallatin Valley, Montana, USA, 1988

Species	Habitat Type		*Sig.*[c]	*Sig.*[d]
	STCO/BOGR[a] 8 Patches	FEID/AGSP[b] 7 Patches		
Group – 1				
Phlibostroma quadrimaculatum	88 (5.69)	0 (0)	*	(*)
Xanthippus corallipes	88 (1.69)	0 (0)	*	(*)
Aulocara elliotti	88 (7.37)	14 (0.02)	*	(*)
Trachyrhachys kiowa	100 (2.65)	14 (0.17)	*	(*)
Ageneotettix deorum	100 (7.91)	29 (0.11)	*	(*)
Psoloessa delicatula	100 (36.30)	29 (0.37)	*	(*)
Group – 2				
Melanoplus infantilis	88 (5.28)	29 (0.12)	n.s.	(*)
Amphitornus coloradus	100 (7.10)	71 (7.25)	n.s.	(n.s.)
Melanoplus sanguinipes	100 (16.72)	100 (30.68)	n.s.	(n.s.)
Melanoplus packardii	88 (0.67)	57 (0.53)	n.s.	(n.s.)
Arphia pseudonietana	75 (0.60)	57 (0.64)	n.s.	(n.s.)
Melanoplus confusus	50 (0.34)	71 (5.18)	n.s.	(n.s.)
Arphia conspersa	38 (0.81)	86 (2.25)	n.s.	(n.s.)
Aeropedellus clavatus	88 (2.54)	100 (6.77)	n.s.	(*)
Group – 3				
Phoetaliotes nebrascensis	38 (1.11)	100 (4.53)	*	(*)
Melanoplus bivittatus	13 (0.35)	86 (4.80)	*	(*)
Melanoplus dawsoni	0 (0)	100 (21.82)	*	(*)

[a] Lower elevation and drier *Stipa comata*/*Bouteloua gracilis* habitat

[b] Higher elevation and wetter *Festuca idahoensis*/*Agropyron spicatum* habitat

[c] Based on non parametric Fisher Exact Probability Test ($\alpha = 0.05$) on frequency of patches within habitat in which species was present

[d] Based on non parametric Mann-Whitney *U*-test ($\alpha = 0.05$) on percent of total grasshoppers collected ( )

AGSP/POSA-STCO h.t., however, suggested that this uncommon type may not be a useful mid-gradient representative (Fig. 1). Similarly, although recognized as technically distinct (Mueggler and Stewart 1980), the proximity of the patches within the STCO/BOGR and AGSP/BOGR may not represent functional differences sufficient to result in the detection of significant grasshopper community composition trends with the organisms studied or the sampling methods employed (Fig. 1).

Much remains for ecologists to consider even within a given herbivore group like grasshoppers. For example, are grasshopper communities equally stable across h.ts. or across patches within h.t.? Literature on grasshoppers suggests that outbreaks of grasshoppers on rangeland may be associated with warm, dry years (Edwards 1960; Gage and Mukerji 1977, and others). It remains to be seen if it is possible to array years along a gradient from wet to dry and show changes in grasshopper community composition, as we did for patches over a similar gradient during one season. Further, little has been done

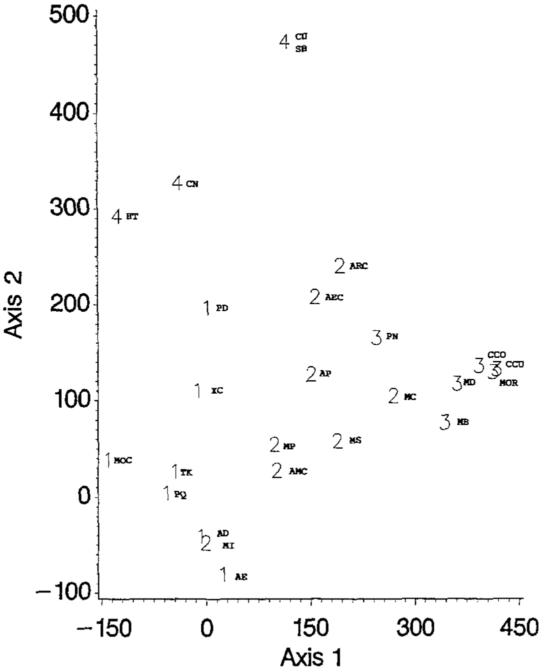

Fig. 5. Detrended Correspondence Analysis of grasshopper species (numbers 1–3 correspond to groups identified in Table 5, Group 4 are species unique to ARAR/AGSP h.t.) for a range of habitat types in Gallatin Valley, Montana, USA, 1988. Eigenvalues for x and y axes are 0.62 and 0.24, respectively. Group 1 species, MOC – *Melanoplus occidentalis*, PQ – *Phlibostroma quadrimaculatum*, TK – *Trachyrhachys kiowa*, AD – *Ageneotettix deorum*, XC – *Xanthippus corallipes*, PD – *Psoloessa delicatula*, AE – *Aulocara elliotti*; Group 2 species, MI – *Melanoplus infantilis*, AMC – *Amphitornus coloradus*, MP – *Melanoplus packardii*, AP – *Arphia pseudonietana*, AEC – *Aeropedellus clavatus*, ARC – *Arphia conspersa*, MS – *Melanoplus sanguinipes*, MC – *Melanoplus confusus*; Group 3 species, PN – *Phoetaliotes nebrascensis*, MB – *Melanoplus bivittatus*, MD – *Melanoplus dawsoni*, CCO – *Chloealtis conspersa*, MOR – *Melanoplus oregonensis*, CCU – *Chorthippus curtipennis*; Group 4 species, CU – *Circotettix undulatus*, SB – *Stenobothrus brunneus*, CN – *Cratypedes neglectus*, HT – *Hadrotettix trifasciatus*

to determine whether populations are higher in all h.ts. during "outbreak years" or if some h.ts. are more prone to periodic grasshopper population eruptions (macroscale example, see Kemp et al. 1989). We believe that the real answers to questions facing rangeland ecologists, regarding the structure of rangeland grasshopper communities in both space and time, will be found in the application and extension of patch dynamics theory.

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References

Anderson NL (1973) The vegetation of rangeland sites associated with some grasshopper studies in Montana. Montana Agr Exp Sta Bull 668

Daubenmire R (1952) Forest vegetation of northern Idaho and adjacent Washington, and its bearing on the concepts of vegetation classification. Ecol Monogr 22:301–330

Daubenmire R (1959) A canopy cover method of vegetational analysis. Northwest Sci 33:43–64

Daubenmire R (1966) Vegetation: identification of typal communities. Sci 151:291–298

Daubenmire R (1970) Steppe vegetation of Washington. Wash Agr Exp Sta Tech Bull:62

Daubenmire R (1978) Plant geography: with special reference to North America. Academic Press, New York, pp 338

Daubenmire R, Daubenmire JB (1968) Forest vegetation of eastern Washington and northern Idaho. Wash Agr Exp Sta Tech Bull:60

Den Boer PJ (1968) Spreading of risk and stabilization of animal numbers. Acta Biotheor 18:165–194

Den Boer PJ (1981) On the survival of populations in a heterogeneous and variable environment. Oecologia 50:39–53

Edwards RL (1960) Relationship between grasshopper abundance and weather conditions in Saskatchewan, 1930–1958. Can Ent 92:619–624

Evans EW (1984) Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. Oikos 43:9–16

Evans EW (1988) Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influence of fire frequency, topography, and vegetation. Can J Zool 66:1495–1501

Evans EW, Rogers RA, Opfermann DJ (1983) Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: night trapping vs sweeping. Environ Ent 12:1449–1454

Gage SH, Mukerji MK (1977) A perspective of grasshopper population distribution in Saskatchewan and interrelationship with weather. Environ Ent 6:469–479

Hanski I (1982) Dynamics of regional distribution and the core and satellite species hypothesis. Oikos 38:210–221

Harvey S, Weaver T (1979) The avifauna of six Montana vegetation types. Proc Mont Acad Sci 38:36–42

Hill MO (1979) DECORANA – A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, New York

Hill MO, Gauch HG (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58

Isely FB (1937) Seasonal succession, soil relations, numbers, and regional distribution of northeastern Texas acridians. Ecol Monogr 7:318–344

Joern A (1979) Resource utilization and community structure in assemblages of arid rangeland grasshoppers (Orthoptera: Acrididae). Trans Am Ent Soc 105:253–300

Joern A (1982) Vegetation structure and microhabitat selection in grasshoppers (Orthoptera: Acrididae). Southwest Nat 27:197–209

Joern A (1983) Host plant utilization by grasshoppers (Orthoptera: Acrididae) from a sandhills grassland. J Range Monog 36:793–797

Joern A (1985) Grasshopper dietary (Orthoptera: Acrididae) from a Nebraska sand prairie. Trans Nebr Acad Sci 13:21–32

Kemp WP, Sanchez NE (1987) Differences in post diapause thermal requirements for eggs of two rangeland grasshoppers. Can Ent 119:653–661

Kemp WP, Kalaris TM, Quimby WF (1989) Rangeland grasshopper (Orthoptera: Acrididae) spatial variability: Macroscale population assessment. J Econ Ent 82:1270–1276

Kent M, Ballard J (1988) Trends and problems in the application of classification and ordination methods in plant ecology. Vegetatio 78:109–124

Kingsolver JG (1989) Weather and the population dynamics of insects: Integrating physiological and population ecology. Phys Zool 62:314–334

Mueggler WF, Stewart WL (1980) Grassland and shrubland habitat types of western Montana. USDA For Serv GTR INT-66

Mulkern GB (1967) Food selection by grasshoppers. Ann Rev Ent 12:59–78

Mulkern GB, Pruess KP, Knutson H, Hagen AF, Campbell JB, Lambley JD (1969) Food habits and preferences of grassland grasshoppers of the north central great plains. North Dakota Agr Exp Sta Bull No 481

Munn LC, Nielsen GA, Mueggler WF (1978) Relationships of soils to mountain and foothill range habitat types and production in western Montana. Soil Sci Soc J 42:135–139

Pfister RD, Kovalchik BL, Arno SF, Presley RC (1977) Forest habitat types of Montana. USDA For Serv GTR INT-34

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 472

Ross RL, Hunter HE (1976) Climax vegetation of Montana: based on soils and climate. USDA Soil Cons Serv Misc Rept

Schoener TW (1986) Mechanistic approaches to community ecology: A new reductionism? Am Zool 26:81–106

Siegel S (1956) Nonparametric statistics: for the behavioral sciences. McGraw-Hill, New York, pp 481

Taylor JA, Friend GR, Dudzinski ML (1984) Influence of sampling strategy or the relationships between fauna and vegetation structure, plant lifeform and floristics. Aust J Ecol 9:281–287

Weaver T (1979a) Climates of fescue grasslands of mountains in the western United States. Great Basin Nat 39:284–288

Weaver T (1979b) Climates of vegetation types of the Northern Rocky Mountains and adjacent plains. Am Mid Nat 103:392–398

White PS, Pickett STA (1985) Natural disturbance and patch dynamics: An introduction. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics: An introduction. Academic Press, New York, pp 3–13

Wiens JA (1976) Population responses to patchy environments. Ann Rev Ecol Syst 7:81–120

Wiens JA (1981) Single-sample surveys of communities: Are the revealed patterns real? Am Nat 117:90–98

Wiens JA (1985) Vertebrate responses to environmental patchiness and semiarid ecosystems. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 169–193