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## Natural enemy assemblages on native and reseeded grasslands in southwestern Montana: a family-level analysis

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NATURAL ENEMY ASSEMBLAGES ON NATIVE AND  
RESEEDED GRASSLANDS IN SOUTHWESTERN MONTANA:  
A FAMILY-LEVEL ANALYSIS

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**ABSTRACT.**—We conducted a 2-year survey, using sweep sampling and family-level taxon identification, of the predatory and parasitoid insects on grassland sites in the Gallatin Valley of southwestern Montana. The 25 sites were divided into 4 habitat classes: 2 native habitat types (*Stipa comata*/*Bouteloua gracilis* and *Festuca idahoensis*/*Agropyron spicatum*) and 2 that had been reseeded with either crested wheatgrass (*Agropyron cristatum*) or smooth brome (*Bromus inermis*). Our major goal was to make quantitative comparisons of the abundance of insects among native and reseeded habitats. Of 51 families in 5 insect orders identified, 7 Hymenoptera (Encyrtidae, Braconidae, Ichneumonidae, Pteromalidae, Eulophidae, Scelionidae, and Torymidae), 3 Hemiptera (Lygaeidae, Nabidae, and Reduviidae), 1 Coleoptera (Coccinellidae), and 1 Diptera (Asilidae) comprised 90% of the natural enemies sampled. Ordination analyses provided no strong evidence that the 4 habitat classes contained distinct overall natural enemy communities. However, contiguous native and reseeded sites usually had relatively different overall natural enemy assemblages, suggesting that vegetation was often a more important correlate of community composition than was close spatial proximity of sites. Furthermore, several common families exhibited differential abundances across habitat classes in one or both years. For example, in 1989, Eulophidae, Pteromalidae, and Torymidae were more abundant on native *Festuca*/*Agropyron* sites, whereas Encyrtidae and Nabidae were more abundant on *Festuca*/*Agropyron* sites reseeded with *Bromus inermis*. Although analyses of insect assemblages classified to the family level provide somewhat limited information on functional ecological differences among habitats, they allow one to survey a broad array of taxa to identify focal groups for future conservation and land management studies.

*Key words:* rangeland, habitat type, Encyrtidae, Braconidae, Nabidae, Lygaeidae, Geocoris.

Even within a limited region, a great diversity of native vegetation assemblages are encompassed by the term *grassland*. In one classification system commonly used for western U.S. grasslands, relatively discrete communities referred to as “habitat types” are defined by their native vegetation assemblages (Mueggler and Stewart 1980), soils, and climates (Weaver 1979a, 1979b, 1980). Natural grassland habitat diversity represented by different native vegetation assemblages is further increased by management practices, such as grazing, burning, and reseeded with exotic grasses (Arenz and Joern 1996), that have implications for both pest management and insect conservation (Kemp et al. 1990b, Bock and Bock 1995, Tscharrntke and Greiler 1995). Some of these management techniques (e.g., burning; Evans 1984) have immediate, direct, and profound

effects upon insects, whereas others may act more indirectly and subtly through alteration of trophic interactions or microclimate.

Grasslands of the Gallatin Valley of southwestern Montana comprise a mosaic of native habitat types that has been further diversified by reseeded many sites with exotic grasses and alfalfa (*Medicago sativa*) during the 1960s and 1970s as part of range management programs aimed at improving early season grazing (Kemp et al. 1990a). To examine the implications of such habitat variation, we have documented the composition of assemblages of selected phytophagous insects on a wide range of sites in the valley for which we have characterized habitat type (Kemp et al. 1990a, 1990b, Bess 1997, Wachter et al. 1998). To complement these species-level diversity studies, we also surveyed families of predatory and

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parasitoid insects present on these habitats. The sites sampled were divided into 4 habitat classes: 2 native habitats (*Stipa comata/Bouteloua gracilis* and *Festuca idahoensis/Agropyron spicatum* habitats) and 2 that had been reseeded with either crested wheatgrass (*Agropyron cristatum*) or smooth brome (*Bromus inermis*). Sites were distributed along an approximately 50-km east–west gradient over which mean elevation decreased by 11% and mean annual precipitation decreased by 22%. Our specific aims were (1) to make quantitative comparisons, among native and reseeded grassland communities, of total abundance of natural enemies and of abundance of specific families and (2) to identify families of natural enemies that were abundant enough to be fruitful for future detailed community studies at our sites.

## MATERIALS AND METHODS

### Site Descriptions

Vegetation at the sites sampled in this study had been previously classified to habitat type by Kemp et al. (1990a) using the scheme of Mueggler and Stewart (1980). All 25 sites sampled are in the northern part of Gallatin County, Montana, USA, within an area defined by latitudes 46°00'N to 45°45'N and longitudes 111°00'W to 111°40'W. The 25 sites include 14 within the *Stipa comata/Bouteloua gracilis* habitat type, 6 of which have been reseeded with crested wheatgrass (*Agropyron cristatum*) and alfalfa (*Medicago sativa*). The 2 habitat classes, referred to here as SB ( $N = 8$ ) and AM ( $N = 6$ ), respectively, occur along a 28-km northeast–southwest line in the western portion of the valley in the vicinity of Three Forks and Logan, Montana (Fig. 1). We also sampled 11 sites within the *Festuca idahoensis/Agropyron spicatum* habitat type, 4 of which had been reseeded with smooth brome (*Bromus inermis*) and alfalfa. These 2 habitat classes, designated here as FA ( $N = 7$ ) and BM ( $N = 4$ ), respectively, occur along a 34-km north–south line in the eastern portion of the valley near the foothills of the Bridger Mountains (Fig. 1). Reseeding with crested wheatgrass or brome had been done to provide grazing earlier in the season, as both grasses begin their growth in early spring. We refer to SB and FA as “native” habitat classes, and AM and BM as “reseeded” habitat classes. Each of the reseeded sites is paired with a contiguous native

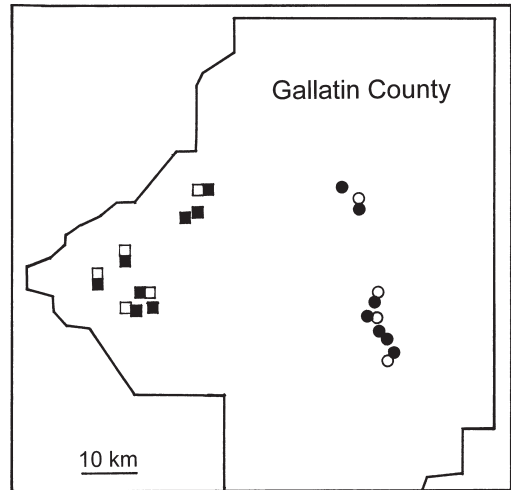


Fig. 1. Map of northern Gallatin County, Montana, showing location of sites: SB sites (closed squares), AM sites (open squares), FA sites (closed circles), and BM sites (open circles).

site. Contiguous sites are given identical site numbers (e.g., SB1 adjoins AM1, FA1 adjoins BM1, etc.). However, native sites designated SB7, SB8, FA5, FA6, and FA7 are not contiguous with reseeded sites.

### Sampling Predators and Parasitoids

We sampled each site 3 times in 1988 and 4 times in 1989. The 3 sample periods in 1988 were 24 May–16 June, 18–21 July, and 22–25 August. The 4 periods in 1989 were 22–27 June, 6–11 July, 31 July–2 August, and 12–18 September. The range of dates during each sample period was constrained by availability of suitable weather. A sample consisted of 200 sweeps with a 38-cm-diameter muslin sweep net, each sweep intersecting vegetation while traversing an arc of 180° parallel to the soil surface. We marked off linear transects at the beginning of the study to ensure that each sample was taken at the same location during each visit. All samples were taken between 0930 h and 1600 h under clear skies (i.e., <15% cloud cover) and light winds (i.e., <25 km · h<sup>-1</sup>). To reduce variation in sampling technique, all samples were taken by the same 2 people. The 1988 samples used in this study were the same as those used to analyze communities of Acrididae (Kemp et al. 1990) and Cicadellidae (Bess 1997) at the same sites.

For each sample we counted the number of individuals from families of predatory and parasitoid insects (Fig. 2). Most families contain only predatory or parasitoid species (Krombein et al. 1979a, 1979b, Borror et al. 1989, Goulet and Huber 1993). However, some families (e.g., Carabidae, Cleridae, Meloidae, Calliphoridae, Sarcophagidae, and Torymidae) contain some noncarnivorous species but were deemed important enough from an ecological standpoint to include in the study. Although these families may have contained a few phytophagous species, they were unlikely to have a major influence on the overall analysis because together they comprised only 5% of the total sample over 2 years. For the Lygaeidae, most of which are phytophagous (Borror et al. 1989), only members of the predator genus *Geocoris* were included.

#### Data Analyses

We made 3 kinds of comparisons among habitats. First, we used detrended correspondence analysis (DCA) using CANOCO (version 3.12; ter Braak 1987–1992) to examine patterns of similarity in predator/parasitoid communities among different sites. DCA is an ordination technique that summarizes count data from a site  $\times$  taxon matrix and arranges it in 2-dimensional space. In site-based DCAs presented here, increased distance between samples in an ordination reflects decreased similarity in the communities at those sites. For DCA analyses we used only families of Hymenoptera, Hemiptera, and Diptera because they were abundant and showed the most variation among sites. Second, we examined whether the 12 most abundant families in our samples differed in abundance among the 4 habitat classes. In this analysis we combined all samples collected at each site, conducting separate analyses for the 2 years. Overall differences among the 4 habitats were examined using Kruskal-Wallis 1-way analyses of variance (with abundance as the dependent variable). We tested for differences in the abundance of specific families between SB and AM sites, and between FA and BM sites using Mann-Whitney tests (with abundance as the dependent variable). Finally, data from the sites at the western end of the valley (SB and AM) were combined and contrasted with combined data from eastern (FA and BM) sites

using Mann-Whitney tests (with abundance as the dependent variable). We chose nonparametric tests because most of the data sets were nonnormal and because we wished to avoid allowing 1 or 2 very large samples to influence the results.

## RESULTS

### Overview of Families Collected

In the 175 samples from both years, 12,977 individuals of 51 families were counted, 4157 in 1988 and 8820 in 1989. Numbers collected in 1989 were greater than in 1988, partly because one more sample was taken at each site in 1989. However, numbers collected in 1989 were still greater than expected based on the number of samples (chi-square goodness-of-fit,  $\chi^2 = 620.7$ ,  $P < 0.001$ ,  $df = 1$ ), primarily because of the huge number of encyrtid wasps collected. Although Encyrtidae comprised only 4% of all specimens in 1988, encyrtids made up 47% of 1989 samples (and 64% of insects collected on SB sites). The most abundant encyrtids in the samples were *Copidosoma bakeri* (Howard) and *C. celsaenae* Howard. In 1989 most (77%) Encyrtidae were collected during September, a period not sampled in 1988. However, the number collected during the 3 earlier sampling periods in 1989 was still over 5 times that collected on corresponding dates in 1988. In addition, Torymidae were absent in 1988 samples but comprised over 3% of the individuals in 1989, appearing in 56% of that year's samples and occurring throughout the summer.

Among 28 families of Hymenoptera collected, 4 constituted 82% of the Hymenoptera and 56% of all insects sampled (Fig. 2). The top 4 families (as well as the Scelionidae) were collected at all 25 sites, with the Braconidae and Ichneumonidae being collected at all sites in each of the 2 years. In contrast, 9 hymenopteran families were represented by  $<10$  specimens each in the combined samples. Among the Hymenoptera there was a significant positive correlation between total number of individuals collected for each family and number of species listed within each family in North America in Krombein et al. (1979a, 1979b;  $r_s = 0.60$ ,  $P < 0.001$ ,  $N = 28$ ). Three families of non-Hymenoptera, the Lygaeidae, Nabidae, and Coccinellidae, comprised another 23% of

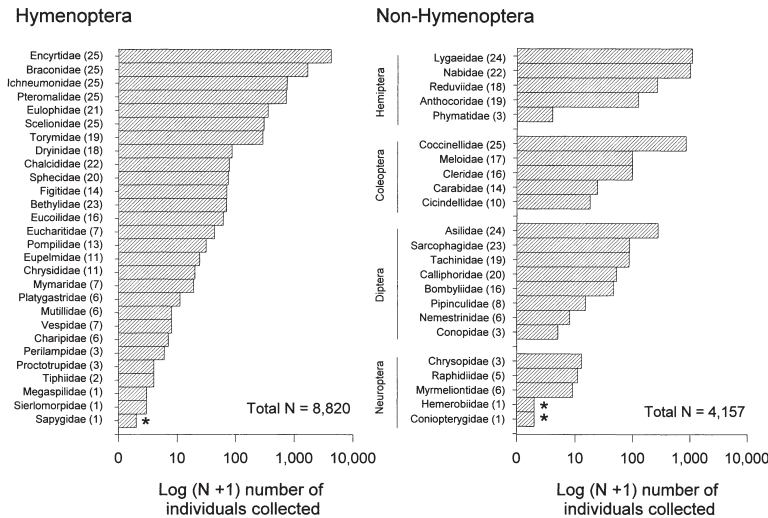


Fig. 2. Relative abundance of families of predatory and parasitoid Hymenoptera and non-Hymenoptera collected over 2 years of sampling. Numbers in parentheses indicate number of sites (out of 25) at which the family was collected. Asterisks indicate families for which just a single individual was collected over the course of the study.

the combined samples and were collected at most sites (Fig. 2). Several other non-hymenopteran families were lower in abundance but were present at most sites, including the Asilidae (24 sites) and Sarcophagidae (23 sites). Six non-hymenopteran families were each represented by <10 specimens.

#### Site Comparisons

In 1988 mean total abundance of predators and parasitoids differed across the 4 habitats, primarily because samples on the eastern sites (FA and BM) harbored more individuals than those in the west (Table 1). This pattern did not hold in 1989 because of the increase in abundance of Encyrtidae in the western side of the valley, where they comprised 64% of the samples from SB sites and 51% of those from AM sites. In neither year did total abundance of all natural enemies differ between reseeded and native habitats at the same end of the valley (Mann-Whitney tests,  $P > 0.05$  in 2 SB/AM and 2 FA/BM comparisons).

Based on their positions in DCA analyses, we found no strong evidence that sites classified a priori into the same vegetation category tended to have distinct overall assemblages of families of Hymenoptera, Diptera, and Hemiptera combined (Fig. 3). In 1988 axis 1 accounted for 39% of the variance, whereas axis 2 accounted for 21%; corresponding values for the 1989 plot were 34% for axis 1 and

12% for axis 2. Small clusters of sites within similar habitat classes did appear on the plots, for example SB sites 1, 3, and 8 in 1988 and SB sites 1, 3, 5, and 6 in 1989. There was also a diffuse cluster of FA sites separated from other habitats on the right side of the 1989 plot. The latter may have been related to the fact that FA was the only class of sites that did not exhibit a large flush of Encyrtidae in 1989. Sites from different habitat classes were often intermingled on the plots. DCA analyses provide little evidence that spatial proximity of sites is important in determining assemblage of families at a site. None of the 6 contiguous pairs of SB and AM sites were each other's nearest neighbors on DCA plots for 1988 or 1989 (in 1989, SB6 was the site most similar to AM6, but not vice versa). Among the 4 contiguous pairs of FA and BM sites, only FA3/BM3 and FA4/BM4 were each other's nearest neighbors on the DCA plots, but only in 1988.

Although DCA provided little support for the hypothesis that overall predator and parasitoid assemblages varied consistently among habitat classes, data reveal several important differences in patterns of abundance for particular families. In 1988, three of the major hymenopteran families exhibited significant variation in abundance across habitat classes (Fig. 4). For the Eulophidae and Scelionidae, overall differences were due to higher abundance on the eastern sites, whereas for the

TABLE 1. Mean numbers of specimens collected (all families combined) within the 4 habitat classes.

Habitat	Number of sites	Mean $\pm$ $s_{\bar{x}}$ collected	
		1988	1989
<i>Stipa comata</i> / <i>Bouteloua gracilis</i> (SB)	8	118.0 $\pm$ 11.5 <sup>a</sup>	356.6 $\pm$ 83.7 <sup>a</sup>
<i>Agropyron cristatum</i> / <i>Medicago sativa</i> (AM)	6	96.9 $\pm$ 14.1	452.5 $\pm$ 90.1
<i>Festuca idahoensis</i> / <i>Agropyron spicatum</i> (FA)	7	237.3 $\pm$ 41.3 <sup>a</sup>	265.0 $\pm$ 42.5 <sup>a</sup>
<i>Bromus inermis</i> / <i>Medicago sativa</i> (BM)	4	312.5 $\pm$ 113.4	278.0 $\pm$ 116.0
Overall Kruskal-Wallis analyses		$P = 0.02$	$P = 0.40$
Mann-Whitney analyses: western (SB + AM) vs. eastern (FA + BM) sites.		$P = 0.003$	$P = 0.15$

<sup>a</sup>Mann-Whitney comparison with reseeded site from same year,  $P > 0.05$ .

Pteromalidae, differences appeared to be due to higher abundance on FA compared to BM sites. In 1989, five hymenopteran families displayed variation across habitat classes. Encyrtidae, by far the most abundant family, was more abundant on western sites, whereas Eulophidae and Ichneumonidae were more abundant in the east. Three families, Eulophidae, Pteromalidae, and Torymidae, were more abundant on FA than BM sites, while the opposite was true for the Encyrtidae.

Among the 5 major non-hymenopteran families in 1988, only the 3 Hemiptera exhibited significant variation in abundance across habitat classes, each for different reasons (Fig. 5). Lygaeidae (*Geocoris* spp.) were relatively low in abundance on AM sites, Reduviidae were abundant only on FA sites, and Nabidae were most abundant within the 2 eastern habitat classes (especially on BM, although numbers were highly variable among the 4 BM sites). In 1989 only Nabidae varied significantly among habitats, again because of greater abundance in the east and on BM sites in particular.

## DISCUSSION

In an analysis of vegetation assemblages at the sites discussed in this paper (Kemp et al. 1990a), we obtained a good separation of all 4 community types using DCA. Native SB and reseeded AM communities had similar total numbers of plant species, but AM sites had a lower proportion of grasses (vs. forbs). SB and AM sites (mean elevation =  $\sim 1350$  m) occur on the western side of the Gallatin Valley where annual precipitation averages about  $\sim 31$  cm  $\cdot$  year<sup>-1</sup>. In comparing native FA and BM communities, we found that FA sites had a higher mean number of plant species and percentage

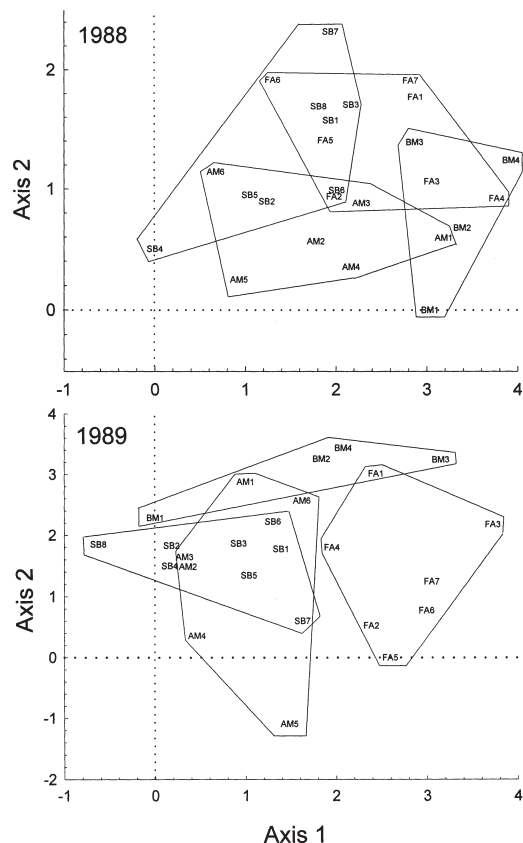


Fig. 3. Detrended correspondence analyses of total samples for 1988 and 1989. Polygons are arbitrarily drawn to surround sites classified a priori as belonging to a particular vegetation class (based on Kemp et al. 1990a).

of grasses. FA and BM sites (mean elevation =  $\sim 1520$  m) occur on the eastern side of the Gallatin Valley, where annual precipitation averages  $\sim 40$  cm  $\cdot$  year<sup>-1</sup>).

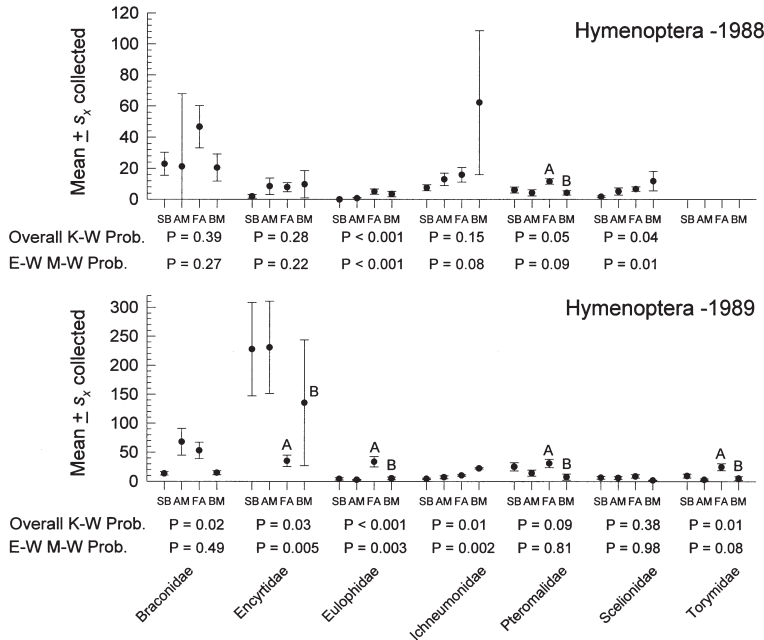


Fig. 4. Mean abundance on each of 4 vegetation types of the 7 most abundant families of Hymenoptera. Overall Kruskal-Wallis (K-W) analyses examine whether abundance of each family varies across the 4 habitat classes. Mann-Whitney (M-W) analyses examine whether abundance for all western (SB + AM) differs from all eastern (FA + BM) sites. Habitat classes with different letters associated with them differ significantly in abundance from classes at the same end of the valley (i.e., SB vs. AM or FA vs. BM; Mann-Whitney tests,  $P < 0.05$ ). See Table 1 for number of sites for each habitat.

DCA analyses of the combined Hymenoptera, Diptera, and Hemiptera provided no strong evidence that the 4 habitat classes contained distinct overall natural enemy communities. However, analyses of specific families give several indications of potentially important differences among habitat classes. Twelve of 23 comparisons (52%) across all 4 habitat classes revealed differences in abundance of specific families, 2 of which showed significant differences during both years (i.e., Eulophidae and Nabidae).

A portion of the differences among habitat classes was apparently associated with reseeding. Eight of 46 (17%) comparisons between native and reseeded habitats revealed differences in abundance of specific families, indicating that reseeding may have an important influence on natural enemy communities. Seven of these differences occurred between FA and BM sites. Eulophidae (1989), Torymidae (1989), Pteromalidae (both years), and Reduviidae (1988) were more abundant on FA sites, whereas Encyrtidae (1989) and Nabidae (1989) were

more abundant on BM sites. The observation that most paired native/seeded sites were not adjacent to one another on the DCA plots also suggests that reseeding can modify natural enemy communities despite the fact that other site characteristics are unaffected by reseeding (e.g. precipitation, elevation, and soil type). At this point it is impossible to determine which ecological correlates of reseeding and habitat fragmentation are responsible for differences in natural enemy assemblages between FA and BM habitats. One major hypothesis would be that, in changing plant community composition, reseeding restructures the phytophagous insect community (Kemp et al. 1990a, Bess 1997) and therefore modifies the resource base for parasitoids and predators (many of which may be specialists). Natural enemy assemblages in native habitats may also be affected by habitat area reduction and isolation from other native habitats with which they could exchange common species. Recently, Kruess and Tschamtkke (2000) found evidence that habitat fragmentation in agricultural landscapes caused greater



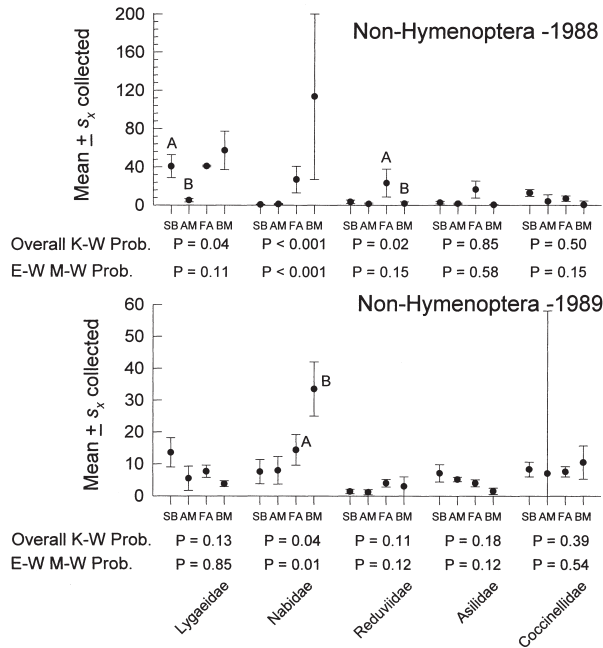


Fig. 5. Mean abundance on each of the 4 vegetation types of the 5 most abundant families of non-Hymenoptera. See Figure 4 for explanation. See Table 1 for number of sites for each habitat.

reductions in parasitoid diversity than in herbivore diversity. Reseeding, through its effect on the physical structure of vegetation, may also alter wind speeds and patterns of insolation near the ground (Geiger 1966). Resulting microclimate changes may have important effects on activity and developmental patterns of small ectotherms, such as insects. For example, dense vegetation may preclude early morning thermoregulation by eliminating ground-level basking sites (Anderson et al. 1979).

According to a strict habitat type classification (in the sense of Mueggler and Stewart 1980), SB and AM sites on the western side of the valley belong to one habitat type (*Stipa comata/Bouteloua gracilis*), whereas the FA and BM sites (in the east) belong to another (*Festuca idahoensis/Agropyron spicatum*). After combining the western and eastern sites into their respective habitat types, 7 of 23 comparisons (30%) revealed differences in abundance of specific families between the western and eastern (higher and relatively mesic) sides of the valley. The most obvious differences were higher abundance of Nabidae in eastern sites in both years and higher abundance of Encyrtidae on western sites in 1989.

There were also instances of significant variation in abundance within habitat classes during a single year, for example, Braconidae on AM sites in 1988, Ichneumonidae and Nabidae on BM sites in 1988, Coccinellidae on AM sites in 1989, Encyrtidae on SB, AM, and BM sites in 1989. Such variation is an indication that (1) site-specific habitat characteristics not incorporated in our habitat classification or (2) local stochastic events may be important in determining predator and parasitoid abundance. Thus, our habitat classes (along with their shared characteristics) are at best rough predictors of local abundance (at the family level). In combination these analyses suggest that reseeded and natural habitat variation (both within and between habitat classes) interact in a complex fashion to influence the composition of natural enemy communities on grasslands.

Phytophagous insect communities also differ among habitat classes discussed in this paper. Using the same 1988 samples from which predators and parasitoids were extracted, Kemp et al. (1990a, 1990b) found that native and reseeded grassland habitats in the Gallatin Valley harbored different grasshopper assemblages. Even stronger differences in grasshopper

assemblages were found when grasslands of surrounding mountain ranges were included (Wachter et al. 1998). In addition, Bess (1997), also using the same 1988 samples (as well as others from 1991 on the same sites), found that leafhopper (Cicadellidae) assemblages differed between native and reseeded sites, and between sites with differing native vegetation. Elsewhere, others have also investigated the effect of deliberate modification of grassland vegetation on insect communities. Rushton et al. (1989) found that reseeded pastures to replace native vegetation reduced diversity of predatory beetles and spiders. Spangler and McMahon (1990) found a higher biomass of sap-feeding Miridae on grasslands reseeded to monocultures. However, they found no difference either between native and reseeded habitats or between reseeded monocultures and bicultures in overall abundance of selected predatory arthropods (i.e., Lygaeidae [*Geocoris*], Nabidae, and Coccinellidae).

In the studies by Kemp (1990a), Spangler and MacMahon (1990), and Bess (1997), focal taxa from grassland samples were identified to species or genus. In the present study we opted for family-level analyses to examine a wide range of taxa (51 insect families in 5 orders). However, counts at the family level may obscure important pieces of ecological information. First, family-level analyses give no indication of within-family diversity or evenness at the species level. Second, members of a single family may fulfill a number of different functional roles within ecosystems (Beattie et al. 1993). At our sites, for example, some Asilidae and Sphecidae prey on grasshoppers (O'Neill 1995), while others take beneficial natural enemies of grasshoppers (e.g., sarcophagid and bombyliid flies; Rees and Onsager 1985) or pollinators (O'Neill and Seibert 1996). Nevertheless, we found habitat-specific differences in abundance of predators and parasitoids that may have important impacts on phytophagous insect communities on grasslands. For example, Encyrtidae are endoparasitoids of scale insects and eggs of other insects and are considered "one of most important chalcidoid families for biological control" (Goulet and Huber 1993). Similarly, many Eulophidae are parasitoids of leafmining insects (Goulet and Huber 1993) and some Scelionidae are parasitoids of grasshopper eggs (Dysart 1995). Other taxa that exhibited differences among habitats may

include generalist predators (e.g., Nabidae and Lygaeidae [*Geocoris*]).

Along with agriculture and urban development, reseeded native grasslands with exotic species, such as crested wheatgrass, smooth brome, and alfalfa, has fragmented native prairie habitats of the western U.S. Although the effect of habitat fragmentation on specific insect communities is usually unknown, the task of documenting the composition of insect communities on multiple sites is daunting. One approach is to choose a narrow array of taxa of known ecological importance on grasslands and to conduct species-level analyses. Even such a focused taxonomic approach can be labor intensive. For example, an analysis of the grasshoppers collected at 39 sites in a single year required identification of nearly 20,000 grasshoppers in 40 species (Kemp et al. 1990a), whereas a similar 2-year study of leafhoppers at 12 sites required sorting over 44,000 specimens to 57 species or genera (Bess 1997). For other taxa we may not always have a priori knowledge of which groups are most abundant at specific sites. Thus, one advantage of a family-level analysis is that it allows one to survey a broad array of taxa to pinpoint groups for "priority attention and commitment of resources" (New 1996) for future conservation and land management studies. In our case we identified several taxa that were abundant and variable in distribution across habitat classes (e.g., Braconidae, Encyrtidae, Eulophidae, Ichneumonidae, Pteromalidae, Scelionidae, Torymidae, Lygaeidae, and Nabidae). Therefore, those conducting studies on similar grassland habitats in the northern U.S. Rocky Mountains might consider these families as fruitful candidates for future species- or generic-level analyses of natural enemy communities.

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