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Temporal Constancy in Grasshopper Assemblies (Orthoptera: Acrididae)

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Abstract
1. Temporal constancy in the structure of grasshopper assemblies (about forty-five species each) from two types of North American grasslands was assessed; one site was followed 25 years and the other 7 years.
2. Densities and relative abundances varied but composition of assemblies based on ranks suggested significant structure when three or more species were included in the analysis.
3. Results compared favorably with other insect herbivore assemblies which have been examined; variability in population change was intermediate along the spectrum of organisms which have been studied.

Keywords: assembly constancy, grasshoppers, population variability, North American grasslands

Introduction

Structure in assemblies of phytophagous insects is not well understood although recent reviews have begun to synthesize the necessary framework (Lawton, 1984a, b; Lawton & McNeill, 1979; Lawton & Strong, 1981; Price, 1983a, b; Strong et al., 1984). Many populations of herbivorous insects fluctuate in size, although some others are relatively constant from year to year. At the community level, the structure of an assemblage over time may

greatly change in terms of both numbers of species and relative abundances of the component species.

Few examples exist which examine the constancy of entire assemblies of phytophagous insects through time (Connell & Sousa, 1983). Lawton (1984a) and Strong et al. (1984) have summarized the constancy of phytophagous insect species inhabiting bracken fern (*Pteridium aquilinum*) (10 years), leafhoppers (Auchenorrhyncha: Homoptera) from a grassland (6 years), and Heteroptera (Acanthosomatidae, Pentatomidae, and Miridae) taken in light traps (4 years). Despite fluctuations in numbers, species ranks are relatively predictable in these studies; common species tend to be typically common from year to year and rare species typically rare. Some exceptions were noted. Based on these studies, it appears that each assembly had a reasonably predictable but not absolutely unchanging structure.

Analyses of temporal constancy from additional assemblies of phytophagous insects are desirable to determine whether the patterns observed to date are representative. Here we examine grasshopper assemblies (Orthoptera: Acrididae) from two nearby types of North American grassland. We test the proposition that the relative abundances of species do not change through time even when overall densities vary. In addition, we describe the variability in densities at one site which was sampled for 25 years.

Materials and Methods

Site descriptions and sampling

Grasshoppers were sampled at two grassland sites in western Nebraska (USA) over a series of years. All species were univoltine, although distinct phenological differences were evident among coexisting species (Joern, 1979, 1982). Although these sites are relatively close (c. 100 km), the grasslands are very distinct types. Many plant species were found in common between sites, and grasses dominated the above-ground biomass. Since sites and sampling methods differed between the sites, each is described separately. To date, approximately forty-five species have been collected at both North Platte and Arapaho Prairie. Only species which are adult in mid-summer collections are included in the analyses. A total of twenty-five species was included for each site. Taxonomic composition and relative abundances among plots at either North Platte or Arapaho Prairie were significantly correlated (Spearman Rank Correlation, $P < 0.001$) so samples were pooled.

North Platte

Sampling was done in an approximately 33 ha site on the south upland escarpment at the west Central Research and Extension Center of the University of Nebraska, North Platte, Nebraska (Lincoln County). Twenty-six sampling sites were established which represented five "plots" on the basis of soil and vegetation characteristics. Detailed descriptions of these plots are found in Mulkern et al. (1969). Most plots represented vegetational groupings expected in a mixed-grass prairie associated with existing micro-topographic relief and soil. Plots were lumped in the analyses because significant correlations of species abundance existed among the plots. One plot was highly disturbed due to winter feeding by cattle as well as various mowing and herbicide treatments and was largely composed

of annual herbs and grasses. This plot (a single site), although unique, contributed several species typical of disturbed areas which are included in the analysis.

Sampling of grasshoppers was performed for 25 years (1960–84). Adults and nymphs are included in the analyses. Samples were taken using a standard 38.1 cm sweep net. During the sample period, fifty sweeps were taken at each site on each date (by Pruess). All sweeps were lumped for the present analyses (i.e., 1,300 sweeps). Sample dates ranged from mid-July to mid-August although the majority were in late July–early August.

Arapaho Prairie

Arapaho Prairie is a 526 ha sandhills grassland reserve located in Arthur County, Nebraska, which is embedded in the large (c. 52,000 km^2), contiguous tract of stabilized, eolian deposited sand dunes and flat interdunal valleys. Vegetation is characterized by a mixture of native tall-grass, mixed-grass, and short-grass prairie species. Detailed descriptions of the vegetation are presented elsewhere (Barnes et al., 1984). Topographic features are representative of upland sandhills prairie with maximum relief from ridgetop to valley of 70 m.

Sampling of grasshoppers was performed for 7 years (1978–84) in early August (by Joern); only adults are included in the analysis. Only relative abundances based on systematic collecting were determined in 1978–79. Grasshoppers were collected as encountered using a sweep net over a fixed period of time. Actual densities were estimated from 1980 to 1984 using sample rings (0.1 m^2) to delineate sample areas. Fifty rings per transect were randomly placed along four transects a day or more prior to sampling; numbers of each species in each ring were counted by very slowly moving along the transects (Joern, 1982; Henry & Onsager, 1978). When vegetation is not dense, as at Arapaho Prairie, this sampling technique is very reliable.

Analyses

Population variability

Variability in population change was quantified in two ways. as the standard deviation of the distribution of log ($N + 1$), where N is population estimate, and as log R, calculated as log N_{i+1}/log N_i (Williamson. 1984).

Relative abundance

Constancy in the taxonomic structure of these assemblies was measured using Kendall's Coefficient of Concordance (*W*), a non-parametric test based on the ranks of the abundances of species among years (Grossman et al., 1982; Siegel, 1956). Relative abundance was calculated as the abundance of species i relative to the total density of all species at the site in that sampling period. If the assembly structure persists, specific ranks of the relative abundances among coexisting species should be similar among years leading to a significant *W*. If assembly structure is not constant, species ranks should greatly vary among years and *W* decrease. Kendall's *W* was calculated for a sequence of assemblies from the top three ranked species (based on the average for all years) until all species were included. This was done to examine the sensitivity of the analysis to the inclusion of species in an

assembly. Correlations among species abundances for all years of the study were also compared to examine pairwise trends.

Multivariate analyses

Cluster analysis (UPGMA) and principal components analysis were performed on the correlation matrix among species at North Platte. In each case the analysis was meant to be of heuristic interest only and we assume correlations to be descriptive statements of the relationships among species. Explicit a *priori* hypotheses related to these analyses were not formed.

Results

Density

Densities and relative abundances of grasshopper species fluctuated among years. Fluctuations in overall densities (all species combined) are shown in Figure 1. Over the 25 years at North Platte, the highest density was 25 times greater than the smallest. The trend is suggestive of overall cycling with c. 20-year periods, but this interpretation certainly requires further data. Estimates of magnitudes of population change for individual species from North Platte are presented (Table 1) as the standard deviation of log $(N + 1)$. Population variability was similar among these species (Fig. 2); no obvious trend was observed between the SD of log $(N + 1)$ and the species rank except for the drop in the SD for the least common species. Mean and variance are not completely independent despite the log transformation.
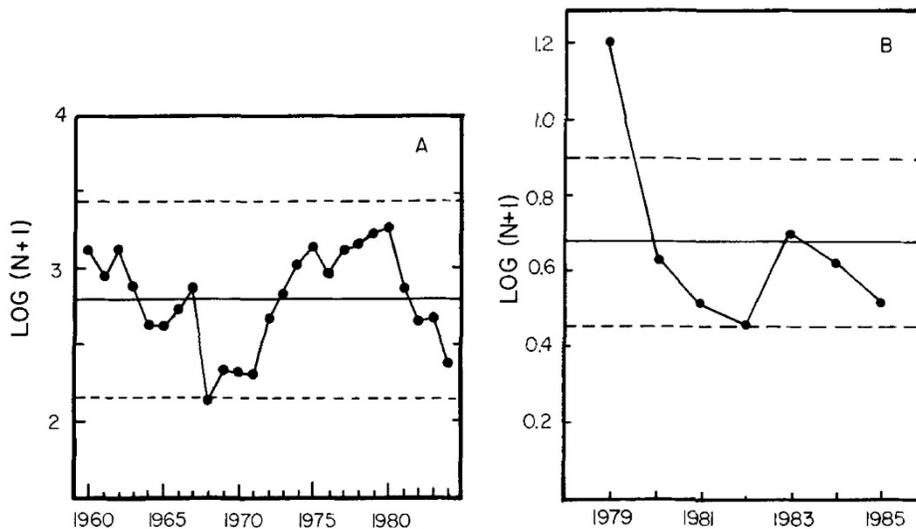

Figure 1. (A) Combined densities (N/1,300 sweeps) of all species from North Platte considered in this study over a 25-year span. Mean density (solid horizontal) and 95% confidence intervals (dashed) for this period are indicated. (B) Densities of grasshoppers (N/m²) from Arapaho Prairie over a 7-year period.

Table 1. Temporal variation in grasshopper population densities and relative abundances at North Platte. Species arc listed in rank order based on average relative abundances over the study period. Statistical significance for the correlation analyses is denoted: * for $P = 0.05$ and ** for $P = 0.01$. General diet classification (Mulkern et al., 1969) is represented as: G, grass; H, herb; and M, mixed grass and herbs. For further details. see text.

| Species	Diet	log $(N+1)$ Mean	log $(N+1)$ SD	log R	Correlation with total density	Relative abundance Mean	Relative abundance SD	PCA coefficients 1	PCA coefficients 2
Phoctaliotes nebrascensis (Thomas)	G	2.10	0.44	0.29	0.51**	0.234	1.34	0.169	−0.214
Ageneotettix deorum (Scudder)	G	1.94	0.51	0.23	0.84**	0.166	0.94	0.313	0.172
Amphitornus coloradus (Thomas)	G	1.62	0.61	0.31	0.85**	0.087	0.52	0.331	0.038
Melanoplus sanguinipes (Fabricius)	M	1.69	0.42	0.26	0.87**	0.08	0.43	0.310	−0.078
Melanoplus femurrubrum (De Geer)	H	1.43	0.44	0.40	−0.09	0.075	0.51	−0.680	−0.013
Opeia obscura (Thomas)	G	1.42	0.44	0.24	0.37	0.064	0.43	0.186	0.362
Trachyrhachys kiowa (Thomas)	G	1.32	0.39	0.25	0.48*	0.042	0.26	0.203	0.326
Melanoplus bivittatus (Say)	H	1.13	0.43	0.38	0.29	0.034	0.32	0.102	−0.317
Hesperotettix speciosus (Scudder)	H	0.86	0.64	0.52	0.03	0.033	0.28	0.036	−0.258
Phlibostroma quadrimaculatum (Thomas)	G	1.16	0.47	0.33	0.67**	0.027	0.16	0.262	0.055
Melanoplus lakimus (Scudder)	H	1.02	0.44	0.37	0.47*	0.027	0.25	0.164	−0.188
Mermiria maculipennis (Bruner)	G	1.08	0.48	0.28	0.73**	0.022	0.14	0.280	−0.048
Melanoplus differentialis (Thomas)	H	0.76	0.60	0.42	0.18	0.018	0.18	0.047	−0.278
Melanoplus keeleri (Thomas)	M	0.81	0.33	0.32	−0.07	0.015	0.10	−0.066	0.112
Aeoloplides turnbulli (Caudell)	H	0.66	0.69	0.37	0.55**	0.014	0.15	0.212	−0.257
Cordillacris occipitalis (Thomas)	G	0.83	0.49	0.28	0.84**	0.011	0.06	0.296	−0.141
Melanoplus packardi Scudder	H	0.79	0.46	0.27	0.63**	0.010	0.06	0.241	−0.074
Chorthippus curtipennis (Harris)	G	0.71	0.50	0.42	0.55**	0.010	0.07	0.217	0.301
Boopedon nubilum (Say)	G	0.53	0.60	0.21	0.31	0.009	0.09	0.105	−0.388
Melanoplus confusus Scudder	M	0.56	0.47	0.35	0.31	0.007	0.05	0.115	0.026
Hesperotettix viridis (Thomas)	H	0.48	0.38	0.28	0.51**	0.005	0.06	0.224	0.195
Hypochlora alba (Dodge)	H	0.33	0.36	0.29	0.33	0.003	0.02	0.106	0.057
Hadrotettix trifasciatus (Say)	H	0.31	0.27	0.34	0.15	0.003	0.02	0.072	0.055
Melanoplus discolor (Scudder)	H	0.20	0.23	0.23	0.09	0.002	0.02	0.025	−0 050
Dactylotum bicolor (Thomas)	H	0.13	0.20	0.16	0.66**	0.001	0.01	0.251	−0.052
% Variance explained								32.20	15.78
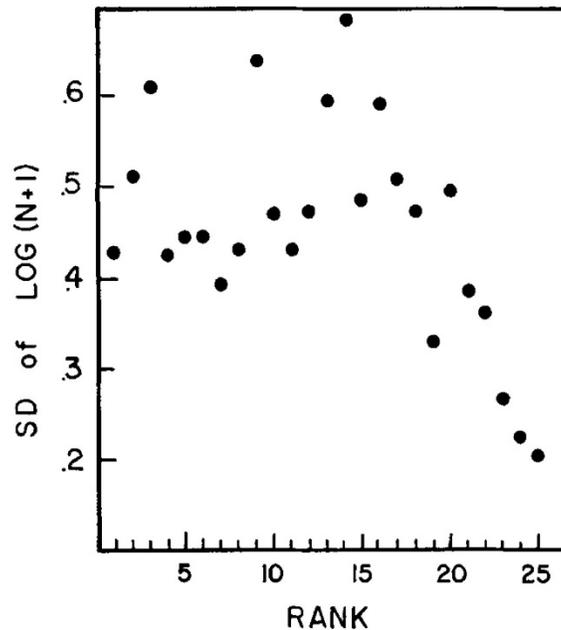
Figure 2. Population variability of the top twenty-five species from North Platte ranked according to average relative abundance.

Densities of many species were positively correlated with the combined density of remaining species (Table 1); note that the density which is used in this analysis does not include the species in question. Only two species had negative correlations (NS in both cases) and 52% (13/25) of the correlation coefficients were significant ($P < 0.05$ and most $P < 0.01$). Relationships among species over this 25-year period at North Platte are shown in a cluster analysis (Fig. 3) based on a correlation matrix constructed from species densities (a copy of the correlation matrix is available from the authors).

A further analysis using principal components analysis (PCA) of the North Platte correlation matrix is included in Table 1. The first two eigenvectors account for 48% of the variance. Coefficients associated with the first principal component are mostly positive (23/25) which may suggest that some environmental factor is affecting all species in a similar fashion. A very strong correspondence exists between those coefficients which are largest in the PCA and species with significant correlations between individual and combined grasshopper densities. The second component is largely a negative relationship between less common grass-feeders and dominant forb-feeders.
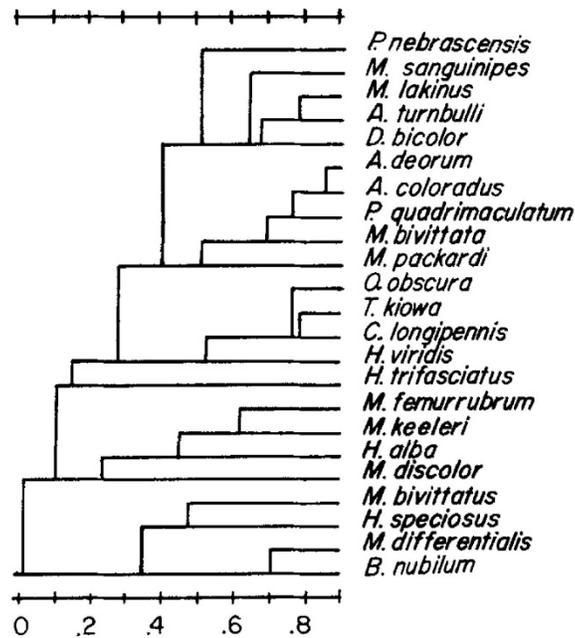
Figure 3. Dendrogram of results from the cluster analysis based on the correlation matrix of North Platte samples.

Relative abundances

Average relative abundances of the grasshopper species from North Platte are listed in Table 1. Many species can be considered uncommon or rare. For North Platte, the top three species constitute 57% and the top five species constitute 74% of the grasshopper assembly, on average. The top three species at Arapaho prairie (regardless of specific taxonomic identity) constitute approximately 60% of the assembly while the top five species constitute nearly 78%.

Constancy of ranking, analyzed using Kendall's *W*, is shown in Figure 4. Constancy of the North Platte assembly was significant beginning with three species. At Arapaho Prairie, any grouping of four or more of the top ranked species from all sites were statistically significant. As more uncommon species are included in the analysis, Kendall's *W* increases. These results may be contrasted with the variation observed in actual relative abundance (rather than just the rank) for the top eight species at North Platte (Fig. 5); similar patterns of change in relative frequencies were seen for Arapaho Prairie.
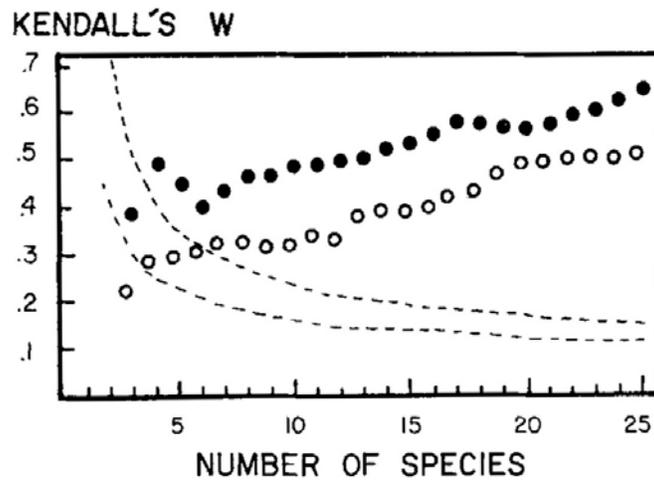
Figure 4. Constancy of grasshopper assemblies from North Platte (●) and Arapaho Prairie (○) based on Kendall's Coefficient of Concordance. Dashed lines indicate statistical cut-offs for the *P* = 0.05 and *P* = 0.01 levels.
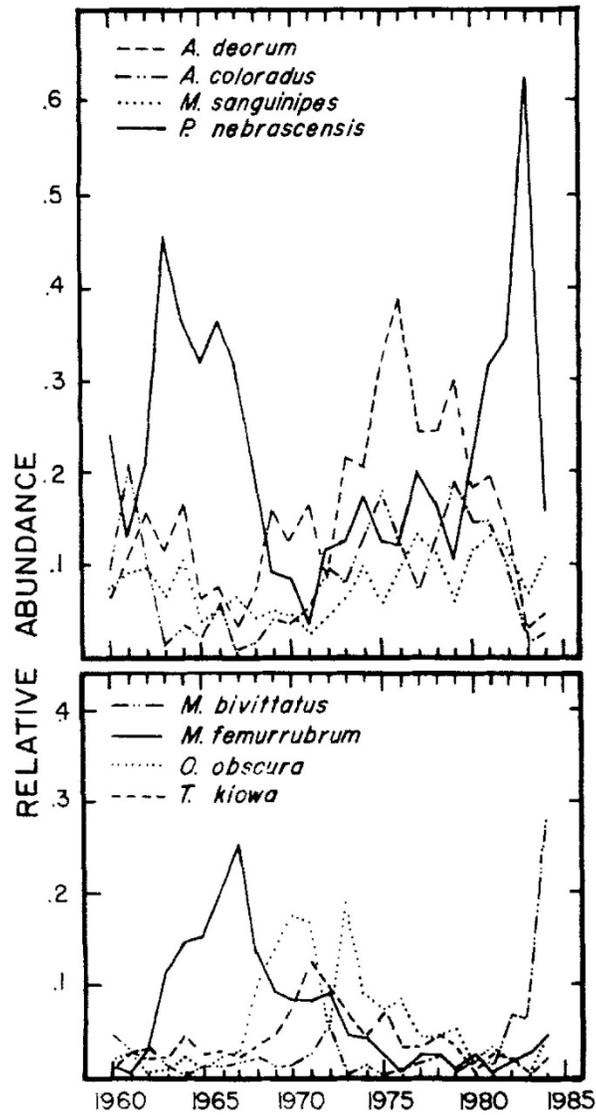
Figure 5. Fluctuation in relative abundance over the 25-year span of the top eight ranked species at North Platte.

Discussion

Overall densities as well as densities of individual species fluctuated from year to year but variability in population size among species was similar except for the most uncommon (Table 1). Total densities of all coexisting species also fluctuated among years. Among the uncommon species, populations may have been so low, if not locally extinct, that they were not sampled in some years. An example at North Platte is *Boopedon nubilum* (Say) which was relatively common from 1960 to 1962 and became uncommon for the remainder of the

study; during eleven of these years the species was not even included in samples. Species which were common, on the average, did not drop out of the samples but did occasionally drop to low levels. Thus, such fluctuations were not unique to rare species. Population variability generally fell within the range previously observed for many insect herbivores (0.4–0.6) and intermediate along the continuum of variability observed for a wide range of species (Connell & Sousa, 1983) with some exceptions in the present study.

At the descriptive level, the type of feeding behavior (grass- versus herb-feeding) may be important in assessing the population dynamics of different grasshopper species. An interesting relationship can be observed by examining the correlations of species with overall grasshopper density (Table 1) in conjunction with the cluster analysis (Fig. 3) and PCA (Table 1). A group of species is significantly and positively correlated with overall density which suggests that some environmental factor (biotic and/or abiotic) is affecting each in a similar fashion. These same species tend to cluster together as expected, and patterns of the cluster analysis are associated with feeding patterns as well. Grasshopper species which primarily feed on grasses tend to fluctuate together as described by the above correlations. Herb-feeding species tend not to be associated with this group nor do these species form an alternate, tight cluster with other herb-feeding species. Of the top ten species, six showed significant, positive correlations with overall density, and only one of these was an herb-feeder even though four of the top ten species fed primarily on herbs.

Feeding behavior alone cannot be singled out to explain these patterns, however. Strong phylogenetic relationships exist that are associated with the type of feeding behavior discussed here. Species in the subfamily Melanoplinae are primarily herb-feeders while the Gomphocerinae and Oedipodinae are primarily grass-feeders (Mulkern et al., 1969; Joern, 1979, 1984). Relationships in species densities among species could be merely coincidental with other attributes among species of these subfamilies and not truly explain the observed patterns.

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