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"Resource Utilization and Coexistence in a Tropical Grasshopper Assemblage: Comparison with Null Models"



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The structure of a grasshopper community in a desert habitat was investigated with particular reference to resource utilization along seasonal time and food resource dimensions. The relative abundance pattern of the assemblage followed MacArthur's broken stick distribution in most of the months.

Five of the eight species analysed showed 70% dietary overlap with at least one other species while seven showed 80% seasonal time overlap with at least one assemblage member. The product overlaps were lower than the value (54%) predicted by MacArthur and Levins but summation overlaps were usually higher than the critical value above which competition is likely to occur. However, despite potential for competition, it seems that competition is infrequent as the food resource is generally not limiting to herbivores. It is suggested that species coexist under nonequilibrium condition due to their dispersal ability, fluctuating environment, predation pressure and patchy habitat. Aggregation may also be responsible for coexistence.

Comparison of patterns of resource utilization in the community with various artificially contrived communities based on null models suggests that biotic interactions do occur. However, mean overlap is not as low as possible suggesting that phylogenetic constraints on resource use may be important.

These are preliminary lecture notes, intended only for distribution to participants.

RESOURCE UTILIZATION AND COEXISTENCE IN A TROPICAL
GRASSHOPPER ASSEMBLAGE: COMPARISON WITH NULL MODELS

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INTRODUCTION

Since the studies of MacArthur (1958) on the niche structure of warblers (*Dendroica*) considerable attention has been paid to investigate interspecific differentiation in the use of resources. Most of such studies have been based on the assumption that competition is the principal organiser and species respond to competition with relatively specific resource utilization patterns for space or food. (MacArthur & Levins, 1967; Pullian & Enders, 1971; Brown & Lieberman, 1973; Yeaton & Cody, 1974, Fraser, 1976; Brown, 1982). In recent years, however, it has been demonstrated that ecologically similar species may coexist without strong competition (Peters, 1976; Weins, 1977; Turner & Polis, 1979; Pianka, 1981; Poysa, 1983). Such a situation exists when predators, parasitoids and environmental fluctuations prevent populations reaching equilibrium densities where competition becomes important (Weins, 1977; Lawton & McNeill, 1979; Caswell, 1978; Strong, 1984).

To explain the observed niche pattern as a first step, it seems appropriate to compare the actual community structure with null models (Caswell, 1976; Connor & Simberloff, 1986; Hoffman & Nitecki, 1987). The null models assume no biological interaction and serve as a null hypothesis because they provide the pattern of niche overlap (in the present context) expected from complete species independence of resource use. Comparison of null models with the structure of natural communities provides an estimate of the effect of biotic interactions. Patterns of plausible ecological significance have some time been reported not to appreciably diverge from random models (Cole, 1951, 1954; Caswell, 1976; May, 1975) while other studies have shown that specific type of biological interactions do play a role in the emergence of the observed patterns (Strong *et.al.* 1977; Inger & Colwell, 1977; Raup *et.al.*, 1976; Sale, 1974; Iakushi & Townsend, 1987). With these facts in view in the present study null models are compared with the observed patterns of overlap in resource utilization by a grasshopper assemblage from a desert habitat to get an understanding of the potentially important ecological interactions.

However, while pursuing the null model approach we fully realize that only experimental studies of natural communities (see reviews by Colwell & Fuentes, 1975 and Pianka, 1976) provide reliable means towards gaining insight of the processes responsible for community organization. In the

experimental approach numerous and often tedious manipulations of various populations are required (Wilbur, 1972; Neill, 1974, 1975; Lane, 1975; McClure & Price, 1976; Rathcke, 1976). However, such manipulations are not feasible for communities with a sizable number of species. On the other hand, the use of specifically designed null models permit alternative explanations of the observed patterns of resource utilization and perhaps discard some possible interactions (Joern & Lawlor, 1980).

This study compares the structure of a grasshopper assemblage determined from two resource dimensions viz. food and seasonal time utilization with simulated assemblages based on various null models to determine the extent of ecological organization in the grasshopper assemblage.

METHODS

Sampling:

The sampling of grasshoppers (Orthoptera) was performed in a natural plant community at Bhawani (2504N - 6648E) distt. Lasbella, Baluchistan where the rainfall is low (about 15 cm). The vegetation is dominated by shrubs and undershrubs including *Aerva javanica*, *Calotropis procera*, *Cassia obovata*, *C. holosericea*, *Heliotropium ramosissimum*, *Sericostoma pauciflorum*. Herb stratum is dominated by forbs like *Sida ovata*, *Tribulus terrestris*, *Citrullus colocynthis*, *Euphorbia* spp. and perennial grasses including *Dichanthium annulatum*, *Cynodon dactylon*,

Desmostachya bipinnata, *Digitaria nodosa*, *Chrysopogon aucheri* and *Cenchrus biflorus*. Annuals generally appear during June to September and their variety and abundance depends largely on the amount of rainfall.

The grasshopper populations were sampled at fortnightly interval in a transect (2km x 15m) by sweep net. The population counts are based on 200 sweeps (catches) at each sampling period. Each sample was preserved separately. The plant species on which grasshoppers were feeding were noted. Diet was determined by analyzing gut contents (Mulkern & Anderson, 1959). Only adults were used to determine resource utilization and sexes were pooled.

Test of randomness in the community:

To test whether the data comes from an organised community or from a random assemblage, Bull's-eye method developed by Hopf & Brown (1986) was employed. The method is used to test whether the abundances of species in the samples of grasshoppers community are distributed randomly. The null hypothesis tested is the "random hypothesis" under which any set of numbers f_i conforming to equation $\sum_{i=1}^S f_i = 1$ is as likely as any other. The f_i in the equation refers to the proportional abundance of the S species in each sample. The scaled distances R are given by:

$$R = \left[\left(\sum f_i^2 - 1/S \right) / \left(1 - 1/S \right) \right]^{1/2}$$

Practically, to compute R first Simpson's (1949) diversity (D) is obtained

$$D = 1 / \sum_{i=1}^S f_i^2$$

then R is computed as:

$$R = \left[\frac{1 - D - 1/S}{1 - 1/S} \right]^{1/2}$$

The scores corresponding to given R and S are subsequently read from a lookup table (Hopf & Brown, 1986).

Abundance patterns:

The relative abundance pattern of species in the community at various time intervals was portrayed in the form of species rank/relative abundance plots, i.e., dominance-diversity curves (Whittaker, 1965; May, 1975). The structure of the community was analysed in greater detail by fitting theoretical models including the niche pre-emption model (Motomura, 1932; May, 1975) and MacArthur's broken stick model (MacArthur, 1957) to verify the assumptions about community design on which these models are based. In the niche pre-emption model the abundance of species ranked from most to least abundant is given by

$$n_i = N C_k K (1-K)^{i-1}$$

where n_i = the number of individuals in the i th species; N = total number of individuals; $C_k = [1 - (1-k)^S]^{-1}$ and is a constant which ensures that $\sum n_i = N$; and $K = 1 - c$, where c is the ratio of the importance value of a species to that of its predecessor in the series of ranked species.

The expected abundance of a species in the broken-stick model is

$$E \left[\frac{n_j}{N} \right] = \frac{1}{S} \sum_{j=1}^S \frac{1}{S-j+1}$$

Breadth and overlap in resource utilization:

An attempt was made to quantify the dietary and seasonal time relationships of the eight most common species. Values of niche breadth and overlap indices were calculated from data on distribution of diet type and seasonal time. The measure used to determine the breadth of resource utilization, i.e., the equitability of the distribution of individuals between the resource states was Levin's (1968) niche breadth formula:

$$B = 1 / \sum_{i=1}^m p_i = 1 / \sum_{i=1}^m N_i^2 / N_T^2$$

where N_i = the number of individuals of the species in question in resource state i , N_T = the total number of individuals in all m resource states and p_i equals the proportion of a species numbers in the i th resource state. Niche breadth values were standardized to range from 0 to 1.0.

The extent of species overlap in resource utilization (O_{ij}) was determined by a symmetric similarity coefficient, previously proposed as a niche overlap measure (Pianka, 1974), as follows:

$$O_{ij} = \sum_{k=1}^m p_{ik} p_{jk} / \left[\sum_{k=1}^m p_{ik}^2 \sum_{k=1}^m p_{jk}^2 \right]^{1/2}$$

where p_{ik} and p_{jk} represent the proportion of the k th resource

states used by the *i*th and *j*th species. Values obtained from this equation are not considered to be competition coefficients but rather measures of overlap in resource utilization (Pianka, 1974).

Average and diffuse overlap

Average overlap is the mean overlap among all species pairs while diffuse overlap is the average overlap experienced by one species from all other species (Pianka's 1974 'diffuse competition'). Average \bar{O}_{ij} and diffuse overlap (O_{di}) were calculated as follows:

$$\bar{O}_{ij} = \frac{\sum_{i=1}^{s-1} \sum_{j=i+1}^s O_{ij}}{\{s(s-1)/2\}}$$

$$O_{di} = \sum_{j \neq i} O_{ij} / (s-1)$$

Summation and product overlaps

Total overlap combines overlap values from separate resource/niche dimensions into one inclusive measure of the overall similarity in between two species and is determined either as summation overlap or product overlap:

$$\text{Summation overlap} = \sum_{r=1}^n O_{ij} = \sum_{r=1}^n O_{ijr} / n$$

$$\text{Product overlap} = \prod_{r=1}^n O_{ij} = \prod_{r=1}^n O_{ijr}$$

When two axes are totally independent, then the overlaps should be multiplied; when two axes are completely correlated the overlaps should be summed. The correlation coefficient between dietary and seasonal time overlap was found to be 0.368. Obviously the two axes are not independent, and summation overlap estimates are probably better estimators of multidimensional resource overlap

(May, 1975; Pianka, 1975). However, both summation and product overlap estimates are reported to indicate which species pair faces greatest overlap.

Null resource utilization models

If competitive interactions are or have been a significant force in shaping community structure, the niches should be hyperdispersed, and average observed overlap in resource use in the actual community should be less than that predicted by the null models. Five null models were constructed by Monte Carlo simulations for evaluating the significance of the observed overlap in resource utilization in the grasshopper community. Comparison of the patterns of resource use for actual communities with simulated communities is based on manipulating the original resource matrix (Lawlor 1980; Tokeshi, 1986). The first four models or reorganisation algorithms RA1 - RA 4 are those developed by Lawlor (1980) while the fifth is developed by the authors. Each randomization algorithm retained a different aspect of community structure while randomly generating the remaining aspects of resource use. In all the five algorithms the electivities of the consumer species were replaced by randomly generated values. The details of the reorganization algorithms are as follows:

RA 1: This algorithm (as well as RA 5) retained the minimum amount of original community structure. Only the original

number of species and the original number of resource states were retained. Observed electivities (including unused resource states or zero electivities) were replaced in each resource matrix entry by random vlaues between 0 and 1 from a uniform distribution. Thus there were far lesser numbers of zeros in the reorganized matrix than in the actual community. Consequently, the niche breadth of each species was increased.

RA 2: In this algorithm all electivities, except zeros, were replaced with random values from a uniform distribution. Thus the qualitative degree of specialization of each species was preserved in the algorithm.

RA 3: This algorithm not only retained the original qualitative degree of specialization of the consumers but also thier their observed niche breadths. Rather than generating electivities the original set of electivities including zeros was permuted for each consumer.

RA 4: Only the non-zero electivities were permuted in this algorithm. Of all the five algorithms this one generated reorganized communities most similar in community structure to the actual community.

RA 5: This algorithm like RA 1 also retained the minimal amount of original community structure. Only the original number of species and resource states were retained. Observed utilizations (including zero) were replaced by numbers drawn from

a Poisson random number generator. For each species the mean utilization value was used to generate random deviates for k resource states using the algorithm of Press *et al* (1986).

To compare the actual and reorganized communities 100 simulations were performed using each of the five reorganization algorithms and pariwise overlaps in diet and seasonal time computed. The average random overlap of each set of 100 simulations was compared with the observed average overlap. The numbers of simulated mean overlap values falling above and below the actual mean overlap and the variance of all pairwise overlaps were also determined. This provided the basis for randomization tests (Sokal and Rohlf, 1969).

R E S U L T S

a) Test of Randomness in the Assemblage:

The distribution of scores in Fig.1 is not uniform as predicted by the random hypothesis. A large peak occurred at 20, indicating that the assemblage tends to be highly uneven and hence is highly nonrandom. The assemblage is characterized by dominance of a few or a single species. The corrected chi-square was found to be 65.66 which is highly significant ($p < 0.001$), indicating nonrandomness in the assemblage.

b) Abundance patterns:

Fig.2 shows the relative abundance patterns of the grasshopper assemblage in different months in the form of

dominance - diversity curves. The results of fitting theoretical models including niche pre-emption model and MacArthur's broken stick distribution as well as Simpson's diversity appear in Table-1. The abundance patterns for all the twelve months approached MacArthur's broken stick distribution based on random niche-boundary hypothesis. Species diversity was generally low ranging between 0.4506 to 0.8572. Diversity was relatively higher during July to October. This roughly corresponds to the monsoon season (July to September). Test of significance (Chi-square test for goodness of fit) with theoretical models (Table-1) shows that for most of the months the grasshopper assemblage did not depart significantly from the broken stick distribution.

c) Breadth of resource utilization (Niche breadth):

Frequency distributions of species' occurrence over seasonal time or food type (plant species) consumed were analysed employing the niche breadth index (B) of Levin (1968). Two species stand out as being very specialized and/or generalized across seasonal time or diet niche axes (Table 2). *Schistocerca gregaria* had a broad niche breadth in the diet niche dimension and a narrow breadth in seasonal time, while *Aiolopus thalassinus* exhibited the opposite trend. Most of the other species had either low or moderate B values in one or both niche dimensions. There appears to be a significant negative relationship between a species' niche breadth in seasonal time and its niche breadth with respect to diet (Spearman's rank correlation = -0.428).

d) Overlap in resource utilization (niche overlap):

Resource overlap values between eight species of grasshoppers based on exploitation of two niche dimensions viz., diet and seasonal time alongwith diffuse overlap values are presented in Table 3. The average overlap between all species pairs was moderately high on diet ($O_{ij} = 0.527$) and on seasonal time niche axis ($O_{ij} = 0.722$). In all thirteen species of plants were identified to be consumed by grasshoppers. These included 5 grasses (Graminae) and 8 forbs. Some species like *Oedaleus senegalensis* and *Aiolopus thalassinus* primarily consumed grasses while others like *Heteracris littoralis* and *Schistocerca gregaria* exploited greater proportion of forbs. Dietary overlap ranged from 0.229 to 0.748. Five of the 8 species analysed showed >70% dietary overlap with at least one other species. *Schistocerca gregaria* and *Oedaleus senegalensis* showed highest overlap along the food niche dimension, followed by *Heteracris littoralis* and *Oxya velox*. Whilst *Oxya velox* and *Aiolopus thalassinus* exhibited lowest overlap in plant species exploitation followed by *Acrida exaltata* and *Aiolopus thalassinus*.

Analysis of 'diffuse' overlap in food dimension experienced by one species with all other grasshopper species showed that *Aiolopus thalassinus* was least similar with all other species in food utilization while *Schistocerca gregaria* was most similar in this respect.

Overlap in seasonal time utilization ranged from 0.437 to 0.904. The average overlap in seasonal time utilization was significantly high ($p < 0.05$) than that of food utilization. Seven out of 8 species showed greater than 80% seasonal time overlap with at least one other species. Diffuse overlap in seasonal time utilization was lowest for *Chrotagonus humalodemus* and highest for *Acrida exaltata*, the latter being common throughout the year.

Complementary overlap:

The unidimensional resource overlap magnitudes presented above probably do not reflect the actual extent of overlap between species. Levins (1968) postulates that as the number of competitive species increases they will eventually have to segregate on more and more dimensions in order to maintain minimal resource overlap. Generally, there are two or three complementary dimensions along which species differentiate and resources are partitioned (Cody, 1974, Schoener, 1974). Species pairs that occupy a similar position along one dimension tend to differ along another (complementary) dimension. Three species pairs exhibited (Table 3) high (>0.7) overlap in one dimension and low (< 0.4) overlap along the other dimension. For example, *Acrida exaltata* and *Aiolopus thalassinus* had a high overlap ($O_{1j} = 0.838$) in seasonal time utilization but very low ($O_{1j} = 0.259$) in diet. Seven species pairs had somewhat low overlap in one dimension and moderate overlap in the other dimension. Three

species pairs had high overlap, while three other species pairs had somewhat low overlap in both the dimensions examined.

To get an idea of how much species pairs overlap in a multidimensional resource space, it is necessary to combine the specific overlap components using the methods described earlier. Table 4 shows that when the two resource dimensions were combined the overall overlap was reduced for each species pair, particularly in case of product overlap. Since real resource dimensions are seldom completely independent of or completely dependent on each other, the actual overall resource overlap might best be assessed as a value falling between the magnitudes obtained from summation and product overlaps (Cody, 1974). Overlaps in the two resource dimensions were found weakly correlated ($r = 0.368$), therefore an intermediate value between $\sum O_{ij}$ and $\prod O_{ij}$ is likely to represent the actual two dimensional resource overlap.

The total diffuse overlap (both product and summation) were also considerably decreased. Summation diffuse overlap ranged from 0.524 to 0.675 while product diffuse overlap ranged from .280 to 0.457. It seems that *Chrotagonus humalodemus* experiences the least diffuse overlap while *Schistocerca gregaria* faces the most.

e) Comparison of actual and reorganised communities.

Comparison of actual food and seasonal time

utilizations with reorganized (simulated) communities are presented in the sequel.

i) Food resource dimension:

The distribution pattern of pairwise overlaps was found to depend on the type of reorganization algorithm employed (Fig.3). Complete randomisation of electivities using random numbers drawn from a uniform distribution resulted in a larger proportion of higher overlaps compared to the original grasshopper community. When observed electivities were permuted among all resource states (RA 3) relatively higher frequency of low overlaps was obtained. Retaining the original zero electivities (RA2 and RA 4) resulted in distributions approaching the shape of the actual grasshopper community. Complete randomisation of utilisation rates based on a Poisson process (RA 5) resulted in a distribution of overlaps similar to that obtained in RA 1, i.e. higher frequencies for larger overlaps. But this distribution was less extreme than that generated by RA 1.

Randomisation test (Table 4) showed that mean overlap of all pairwise comparisons in the actual community were significantly different than those obtained in simulated communities generated by any of the reorganisation algorithm at least at the probability level of 0.1 (three were significantly different at $p = 0.5$). The mean overlap in the actual community was greater than that obtained in RA 2, RA 3 and RA 4 but less than those obtained in the complete randomization, viz. RA 1 and

RA 5. Randomization process that retained both the zero utilization structure and the original nich breadth (RA 4) had mean overlap closest to that of actual community.

Mean variance of pairwise overlaps were significantly lower in reorganization algorithms 1 and 5 where simulated communities were based on complete randomization. The mean variance of those artificially contrived communities which retained the original zero electivities (RA 2 and RA 4) were closest to that of actual community. Interaction between mean overlap and variance is such that when mean overlap is high, the variance tends to be low.

ii) Seasonal time utilisation:

The distributions of pairwise overlap in seasonal time (Fig. 4) are essentially similar to those obtained for diet. High overlap frequencies were predominant when all utilisation rates were either sampled from a uniform or a Poisson distribution (RA 1 and RA 5) and low overlaps were comparatively more common when actual electivities were randomly permuted among the resource states (RA 3). Preserving the original zero utilisation structure (RA 2 and RA 4) resulted in closely similar distributions but these did not correspond with the actual distribution of overlaps.

Mean overlaps obtained in RA 2, RA 3 and RA 4 were significantly lower than that of the actual community. The mean

overlaps in completely randomised communities (RA 1 and RA 5) were higher than the actual community mean overlap although not significantly so ($p < 0.20$).

The mean variances of completely randomized simulated communities (RA 1 and RA 5) were significantly lower than that of actual community (p at the most 0.05). Wherever zero utilization structure was retained (RA 2 and RA 4) the mean variances did not differ significantly from the mean variance of actual community. Niche breadth seems to influence variance since rearranging original utilizations among all resource states (RA 3) increased the variance over that of the actual community although not significantly so ($p = 0.06$). Mean overlap and mean variance were found to be negatively correlated.

DISCUSSION

Abundance pattern:

The relative abundance pattern of the community followed MacArthur's (1957) broken stick distribution. Since the proposition of this model, data sets have been gathered which both confirm and reject its validity (King, 1964; DeVita, 1979). Close fits to this distribution are primarily found in narrowly defined, K - selected, taxonomically related organisms (King, 1964, Whittaker, 1972). Whilst assemblages of r-selected species with fluctuating populations are generally shown not to fit this model (Bush & Holmes, 1983). The present results are therefore

unique in that the broken stick distribution is shown to fit r-selected, taxonomically related organisms with fluctuating populations. However, Boosma & Loon (1982) have found good fit to this model in ant communities. In terms of niche, broken stick distribution can be explained by three different models (c.f. Pielou, 1977 Giller, 1984). MacArthur's original model, as designed, assumes a community of competing species. However, the same distribution can be predicted by theoretical models that do not invoke competition. In case of assemblages of herbivorous organisms such as grasshoppers competition is perhaps minimal (see below).

The 'broken stick' distribution is to be expected whenever a small, ecologically homogeneous group of species, such as the grasshopper assemblage, divides a fixed amount of some major resource randomly amongst themselves (Giller, 1984). It is not necessary to invoke competition as a regulatory mechanism, but a good fit to this model suggests that a single factor plays a predominant role in structuring the community.

Resource utilization and coexistence:

Niche breadth values for food utilization indicate that *Schistocerca gregaria* and *Chrotagonus homalodemus* were generalists while *Heteracris littoralis* and *Acrida exaltata* were specialists. With respect to seasonal time resource dimension *Aiolopus thalassinus* and *Acrida exaltata* were generalist while *Schistocerca gregaria* and *Oxya velox* were specialists. Species

which were generalist in one resource dimension were usually found specialist in the other dimension.

Despite high overlap values, at least in one resource dimension, it is unlikely that widespread competition occurs among the members of this grasshopper assemblage. Mere overlap in resource use between species does not necessarily imply competition (Vandermeer, 1972; Sale, 1974). Likewise, intensity of competition need bear no relation to the degree of niche overlap (Davies *et al.*, 1979). In addition, overlap on one resource dimension may indicate diversification in other ways. Only two resource dimensions were examined—seasonal time and diet. It is likely that grasshopper species may have segregated in some other resource dimension such as microhabitat (Joern, 1979). If food is considered as a limiting factor, only three of eight species were found to have a diffuse overlap value greater than the 54% limit predicted by MacArthur & Levins (1967) for coexistence without competition. However, 16 out of 28 pairs showed > 54% overlap in the food dimension, although the average overlap (\bar{O}_{ij} = 0.527) was less than the critical value. Of the 28 pairs 18 summation overlaps and only 7 product overlaps exceeded the predicted value of 54% which allows for coexistence without competition. Considering that the true overlap lies somewhere between the values of product and summation overlaps, probably more than half of the paired combinations did not reach the critical overlap for competition to occur.

The importance of competition in structuring the grasshopper community was assessed using null models. Competitive models of community structure maintain that hyperdispersed patterns of resource utilization are evolutionary results of past competition (MacArthur 1972; Schoener, 1974). The major outcome expected from this relationship is the decreased level of overlap in resource utilization. Thus, if the average resource overlap of an actual community is substantially lower than that of an artificially contrived random community, competition must be a significant force. Comparison of the actual resource utilization distributions for both diet and seasonal time with the completely randomized simulated communities (RA 1 and RA 5) showed that the average overlap of actual community was markedly lower than that of simulated communities. Though this result indicates some resource partitioning, comparisons of actual community with other reorganized communities (RA 2 - RA 4) suggest that decreased mean overlap does not fully explain the interactions involved in community organization. The observed resource utilization matrix represents the peculiarities of resource use by the grasshopper species. Two important features of the resource matrix are the zero structure (non utilization of resource states) and niche breadth. The mechanisms responsible for these two features may indicate how important competitive interactions are in structuring the community (Joern & Lawlor, 1980). When the observed electivities were randomly permuted among all resource states (RA 3), for both diet and seasonal time, the resulting

mean overlap decreased significantly compared to that of actual community. Preserving the original zero electivities, by either replacing (RA 2) or by permuting also markedly decreased the mean overlap compared to that obtained in complete randomization (RA 1 and RA 5). The mean overlap resulting from RA 4 was closest to that of actual community along the food dimension.

Mean overlap and competitive interactions are expected to be minimum if the component species of a community could specialize on any set of resources (Joern & Lawlor, 1980). However, due to phylogenetic constraints (or design constraints (Stearns, 1977) this could not be achieved in the assemblage studied. In the grasshopper assemblage, for example, members of subfamily Oedopodinae primarily consume grasses while those belonging to Catantopinae primarily consume forbs. Thus phylogenetically related species have similar resource utilization pattern which tends to increase mean overlap of the actual community compared to that of RA 3. Despite this force that increases similarity in resource utilization, the members of the assemblage still tend to diverge in the results of RA 4 simulation where only nonzero electivities were rearranged, particularly in case of seasonal time overlap.

There are a number of other reasons to disregard competition as a predominant force in structuring the grasshopper community. Most predictions of competition theory assume that the community is at equilibrium. Insects are small, short lived, and

are highly sensitive to spatial and temporal environmental variability (Weins, 1977). Because of these characteristics and other factors such as predation and parasitoids their populations seldom reach equilibrium densities at which competition becomes important (Lawton & McNeill, 1979; Caughley & Lawton, 1981; Faeth et al., 1981; Strong, 1984). Fluctuations in the populations of phytophagous insects may be due to their involvement in coupled oscillation systems such as host-parasite interactions (Anderson & May, 1980), predator-prey interactions (Hassell, 1978) or plant-herbivore interactions (Crawley, 1983). Herbivore systems, which often show much overlap, are subject to extreme predation pressure that partially suspends the effects of competition and permits more overlap and hence greater coexistence. (Roughgarden & Feldman, 1975). In addition to influencing prey population dynamics, predation may also influence the spatial distribution of prey. These in turn affect community structure and function (Hughes, 1980).

The applicability of a nonequilibrium hypothesis to the determination of grasshopper community structure is predicted upon a number of necessary conditions to which the grasshoppers seem to conform. One important condition is the ability to disperse and exploit new microsites and microhabitats. The dispersal capability of grasshoppers has been well documented (Johnson, 1969; Magor, 1989). Several workers have described situations which allow coexistence in a nonequilibrium state when dispersal

is important. Through a mathematical model, Skellam (1951) demonstrated that among species with low reproductive rates but high dispersal ability coexistence can be maintained under nonequilibrium condition. Nonequilibrium coexistence has also been shown in mathematical models incorporating habitat patchiness and dispersal ability (Cohen, 1970; Levins & Culver, 1971; Horn & MacArthur, 1972; Levin, 1974). Secondly, in case of competitively weak species (fugitive species) under catastrophic or highly fluctuating environmental conditions coexistence is possible if the species can disperse easily (Hutchinson, 1953).

Habitat patchiness and aggregation of grasshoppers also appear to be important factors facilitating coexistence. Aggregation is such a prominent characteristic of insects that it is often regarded as a life history trait (Taylor, 1971). Herbivorous insects generally make their living on patches of preferred food plants surrounded by unpalatable vegetation and bare ground (Kareiva, 1986). Clumped plant population structures in arid regions have been recorded by a number of researchers (Greig - Smith & Chadwick, 1965; Anderson *et al.*, 1969; Shaukat *et al.*, 1983). Aggregation in insects may be due to variety of factors (Southwood, 1978). In case of the grasshopper community it has been found that the aggregation pattern of some of the grasshopper species corresponds with the spatial pattern of food plant populations (Shaukat & Khan, in preparation). Computer simulation of model communities (Atkinson & Shorrocks, 1981) has

shown that in patchy environment the aggregative behaviour of insect species makes coexistence possible without niche differentiation.

In conclusion, there are several reasons to support the notion that competition is not a major organizing force within this assemblage. When factors known to influence competition are considered, it seems possible that competition is too infrequent minimal, or nondirectional to cause competitive avoidance or displacement. Coexistence is facilitated by a number of factors including predation, dispersal, environmental fluctuations, habitat patchiness and aggregation of grasshopper species. This assemblage is not unique in lacking competitive organization. Phytophagous insects, which are seldom food limited, are among the least likely groups to exhibit patterns predicted by competition theory.

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LEGENDS OF FIGURES

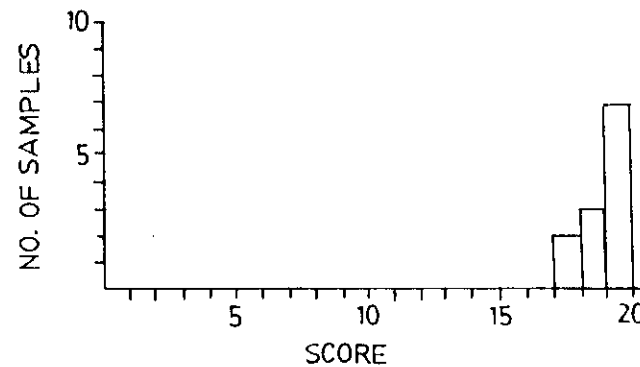
Fig. Distribution of scores for relative abundance of grasshoppers in 12 months.

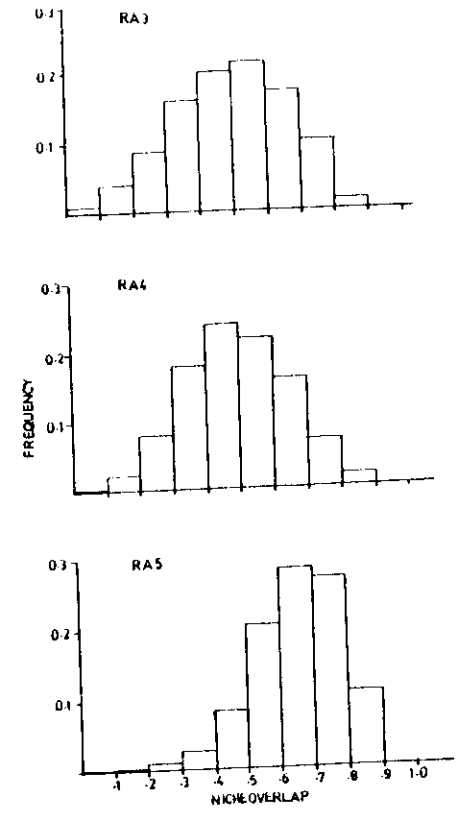
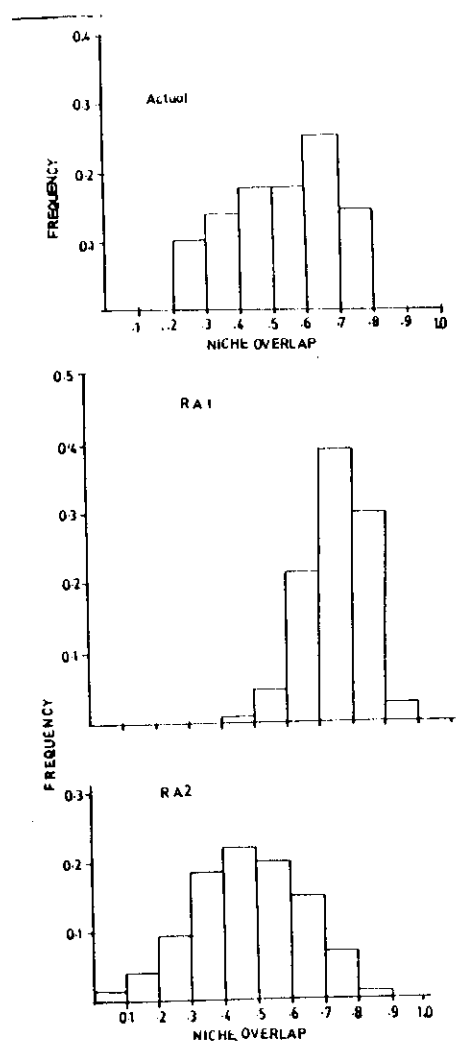
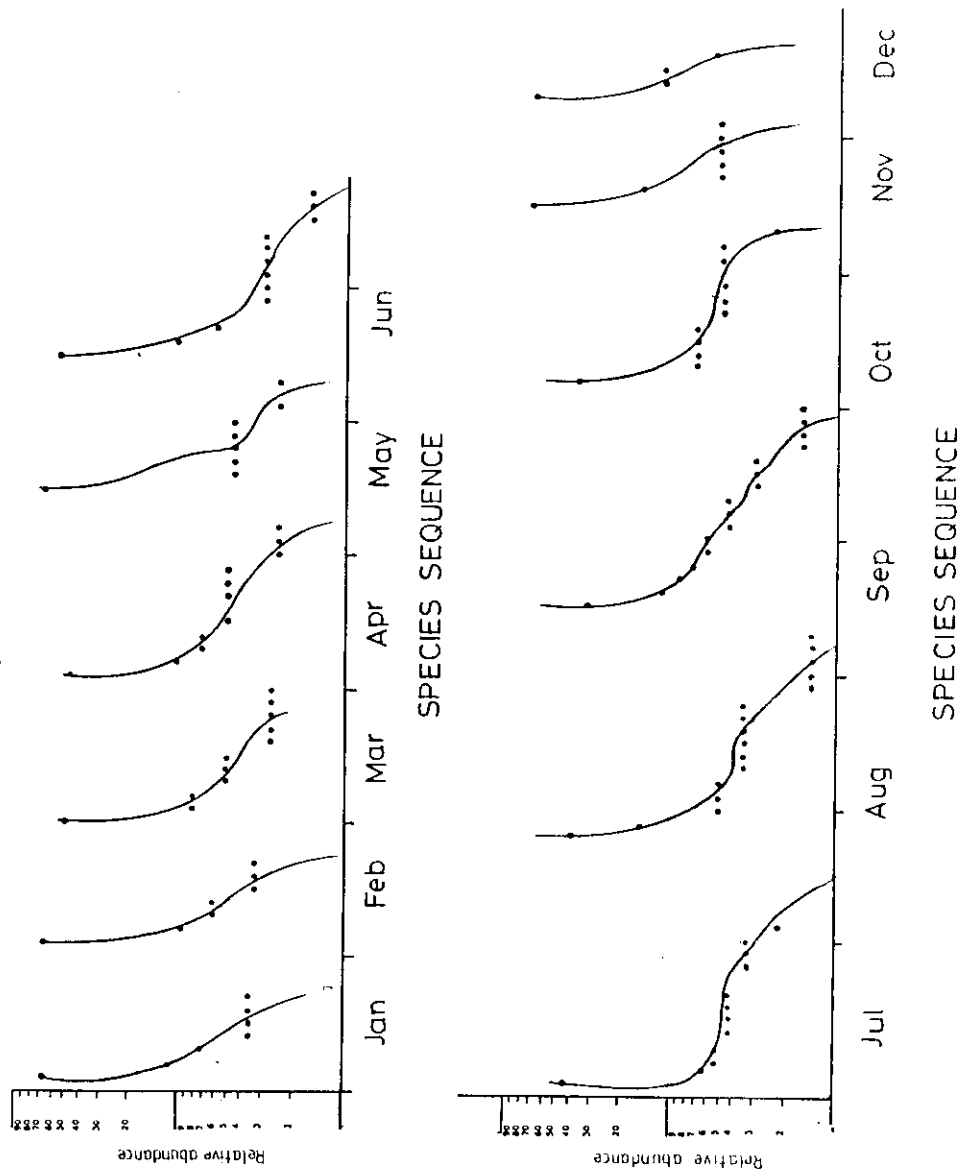
Fig.2 Dominance - diversity curves for the grasshopper assemblage in different months.

Fig.3 Distribution patterns of pairwise overlaps (food dimension) for the actual community and for the simulated communities generated by reorganization algorithms (RA 1 to RA 5).

Fig.4 Distribution patterns of pairwise overlap (seasonal time dimension) for the actual community and for the simulated communities generated by reorganization algorithms (RA 1 to RA 5).

Fig 1





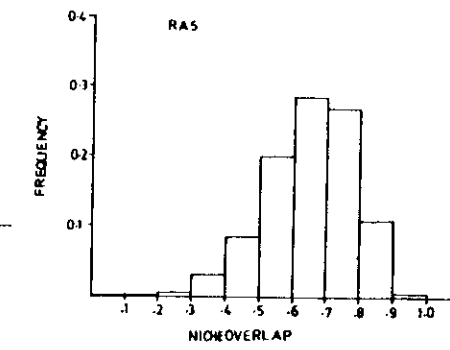
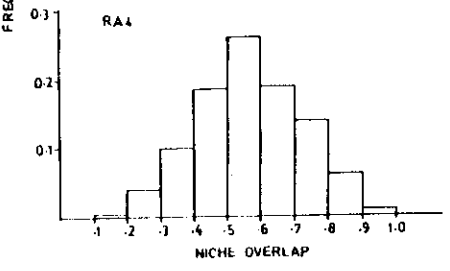
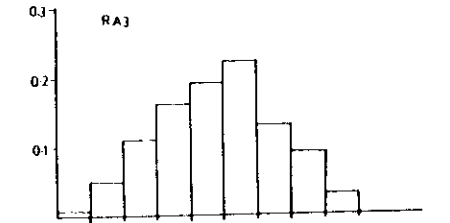
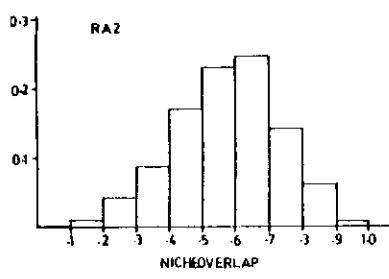
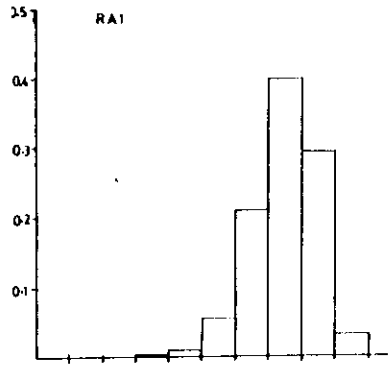
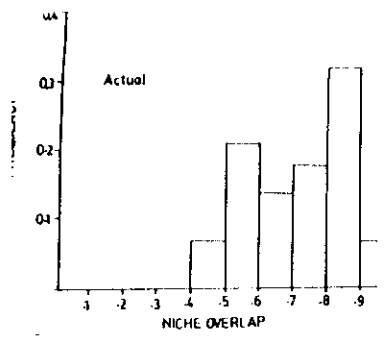


Fig. 4.

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Table 1. Simpson's diversity value and Chi-squared test of goodness of fit of the monthly observed relative abundance pattern of the grasshopper assemblage to the niche pre-emption and MacArthur's broken stick models.

Month	No. of Species	Simpson's diversity	χ^2 for pre-emption model	Probability of goodness of fit	χ^2 for broken stick model	Probability of goodness of fit
Jan.	7	0.547	45.99	< 0.0001	10.15	> 0.1
Feb.	7	0.533	51.16	< 0.0001	12.24	> 0.1
Mar.	11	0.707	144.05	< 0.0001	13.52	> 0.1
Apr.	12	0.784	75.63	< 0.0001	10.39	> 0.4
May	9	0.519	547.63	< 0.0001	9.14	> 0.3
Jun.	13	0.669	997.91	< 0.0001	36.97	< 0.0003
Jul.	18	0.786	1378.82	< 0.0001	41.74	< 0.0008
Aug.	16	0.802	238.59	< 0.0001	18.77	> 0.2
Sept.	16	0.857	51.63	< 0.0001	7.91	> 0.9
Oct.	12	0.812	68.75	< 0.0001	13.12	> 0.2
Nov.	7	0.626	21.65	< 0.001	5.59	> 0.4
Dec.	4	0.450	3.55	> 0.3	3.52	> 0.3

Table 3. Matrix of overlap in resource utilization. Values above the diagonal are for diet; values below the diagonal are for seasonal time. Od_i = Diffuse overlap on one species from all other species.

Species	Ae	Hi	Ov	Sg	Os	Ah	Ch	At	Od_i
<u>Acrida exaltata</u>	-	0.726	0.714	0.555	0.471	0.574	0.454	0.259	0.536
<u>Heteracris littoralis</u>	0.904	-	0.741	0.689	0.555	0.458	0.286	0.377	0.548
<u>Oxya velox</u>	0.848	0.885	-	0.629	0.458	0.660	0.304	0.229	0.534
<u>Schistocerca gregaria</u>	0.849	0.889	0.889	-	0.748	0.639	0.566	0.598	0.632
<u>Oedius senegalensis</u>	0.889	0.921	0.869	0.767	-	0.389	0.452	0.307	0.483
<u>Acrotyus humbertianus</u>	0.708	0.522	0.660	0.563	0.596	-	0.606	0.671	0.571
<u>Chrotacanus homalodemus</u>	0.539	0.576	0.437	0.441	0.600	0.623	-	0.659	0.475
<u>Aiolopus thalassinus</u>	0.838	0.726	0.676	0.615	0.758	0.817	0.791	-	0.443
Od_i	0.797	0.776	0.752	0.718	0.772	0.641	0.572	0.746	-

Table 2. Breadth of resource utilization values (Levins, 1968) for eight species of grasshoppers with respect to seasonal time and diet.

Species	B_1	B_1
	(Season)	(Diet)
<u>Acrida exaltata</u>	0.650	0.328
<u>Heteracris littoralis</u>	0.421	0.298
<u>Oxya velox</u>	0.378	0.392
<u>Schistocerca gregaria</u>	0.352	0.746
<u>Oedius senegalensis</u>	0.416	0.555
<u>Acrotyus humbertianus</u>	0.491	0.590
<u>Chrotacanus homalodemus</u>	0.417	0.611
<u>Aiolopus thalassinus</u>	0.881	0.471

Table 5. Comparison of actual community diet and seasonal time overlap matrices with Monte Carlo simulated (reorganized) overlap matrices based on null models (reorganization algorithms) for resource utilization. Overlap summary statistics include mean overlap and mean variances of 100 simulations for each comparison.

Algorithm	Mean Overlap	Mean Variance	\bar{O} less than observed	\bar{O} greater than observed	\bar{V} less than observed	\bar{V} greater than observed
a) Diet (8 species, 13 resource states)						
Actual	0.527	0.025				
RA 1	0.748	0.007	0	100	100	0
RA 2	0.472	0.027	96	6	34	66
RA 3	0.492	0.028	92	8	29	71
RA 4	0.493	0.023	95	5	67	33
RA 5	0.650	0.016	2	98	90	10
b) Seasonal time (8 species, 12 resource states)						
Actual	0.722	0.022				
RA 1	0.752	0.008	13	87	100	0
RA 2	0.569	0.024	100	0	40	50
RA 3	0.479	0.032	100	0	6	94
RA 4	0.569	0.024	100	0	41	59
RA 5	0.754	0.013	19	81	96	4

Table 4. Matrix of summation overlap and product overlap in resource utilization of 8 grasshopper species. Values below the diagonal are for product overlap; values above the diagonal are for summation overlap.

Species	Ae	HI	Ov	Sg	Os	Ah	C	At	$\sum O_{ij}$
<u>Acrida exaltata</u>	-	0.815	0.781	0.702	0.680	0.641	0.497	0.549	0.666
<u>Heteracris littoralis</u>	0.656	-	0.813	0.794	0.738	0.490	0.431	0.551	0.662
<u>Oxya velox</u>	0.605	0.656	-	0.759	0.663	0.660	0.370	0.452	0.642
<u>Schistocerca gregaria</u>	0.471	0.619	0.559	-	0.757	0.601	0.503	0.607	0.675
<u>Oedipus senegalensis</u>	0.419	0.511	0.397	0.573	-	0.492	0.526	0.533	0.627
<u>Atractylus humbertianus</u>	0.406	0.239	0.436	0.360	0.231	-	0.614	0.744	0.606
<u>Chrotagonus homalodemus</u>	0.245	0.165	0.132	0.249	0.271	0.377	-	0.725	0.524
<u>Aiolopus thalassinus</u>	0.217	0.274	0.154	0.368	0.233	0.548	0.521	-	0.594
$\bar{T}O_{di}$	0.431	0.446	0.420	0.457	0.376	0.371	0.280	0.331	-

