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ESTIMATION OF SPATIO-TEMPORAL REARRANGEMENT IN A PATCHY HABITAT AND ITS APPLICATION TO SOME AUCHENORRHYNCHA POPULATIONS

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SUMMARY

(1) An ordination (PCA)-based method was developed to estimate the degree of spatio-temporal rearrangement between two groups of organisms.

(2) The ordination was based on the relative occurrences of the organisms among sampling sites. Rows of the data matrix (variables) represented the different sampling sites, and columns (PCA-objects) represented the subsequent times of sampling.

(3) The spatial rearrangements were detected from the position of objects on scattergrams of the PC-analysis.

(4) The degree of rearrangement of real organisms was estimated by a calibration curve constructed using simulated rearrangement of computer-made populations.

(5) The method was applied to selected Auchenorrhyncha populations. Generations of the oligophagous *Kosswigianella exiqua* Boheman and the summer diapausing *Mendrausus pauxillus* Fieber showed intragenerational spatial rearrangement. A third species, *Turrutus socialis* Flor, showed more than 25% of intergenerational spatial rearrangement, in connection with the wider host plant spectrum.

(6) These different strategies reflect the direction of adaptation, namely adaptation to the whole patchy habitat or to the single patches themselves. The developed method seems to be useful in distinguishing the two possibilities.

INTRODUCTION

The changes in spatial distribution can be the result of adaptation of the population studied, because the adaptation of insects is often accompanied by the changes in moving behavior. These changes can be caused by ecological migration, in other words 'population redistribution by movement' (Taylor & Taylor 1983) and/or the uncorrelated population dynamics in the different localities (Hanski 1989).

The changes in spatial distribution can be described easily when the majority or the whole insect population is involved, e.g. the migration from crops to grasses and back (Raatikainen 1971; Blocker, Harvey & Launchbaugh 1972), or when the preferred habitats are of different character (e.g. zonation) (Denno & Grissel 1979; Györfy & Kincsek 1986; Brown *et al.* 1985). It is more complicated to detect a rearrangement of spatial pattern when this occurs on a mosaic-like habitat, especially when the boundaries of the patches are not sharp. However, the tolerance or adaptive responses of insect populations are at their most effective in such

responses, as 'too much dispersal destroys ecotopic adaptation, too little leads to excessive competition, and vulnerability to catastrophic habitat change' (Taylor 1985). The degree of change in spatial distribution can be regarded as the manifestation of adaptation. Our aim was to estimate this degree in a patchy habitat. Our starting ideas are as follows.

A population living in a patchy habitat can adapt to the whole patchy habitat, or to the single patches themselves, i.e. to the habitat or to the microhabitat (we regard the habitat as the area that provides the resource requirements for the whole life of a population). In the first case a population can have different habitat requirements. The population can satisfy these requirements in an active manner, looking for the best suitable patches. The spatial distribution of such a population changes considerably in changing habitat. In the second case, when the subpopulations belonging to a population persist in their patches, they have to stand the changes, e.g. decreasing suitability of the host-plant or microclimatic changes. The success of adaptation can be characterized by a measure of the subpopulations not being forced to leave the occupied patches, i.e. of a decrease in their mobility. In this case, the adaptive mechanism can be some form of dormancy. If we can estimate the changes in spatial distribution of a population in patchy habitat, we can estimate the position of the population on the habitat–microhabitat adaptation scale.

Various indices of dispersion have been used to describe the seasonal changes of spatial patterns, e.g. variance/mean, mean crowding, Taylor's power law (Southwood 1978). However, the spatial events cannot be followed by these indices. Multivariate methods provide a better description of such events, so we chose the centered, standardized form of Principal Component Analysis. Our main aims were: (i) to find a method for estimating the changes in spatial distribution; (ii) to test the method on different Auchenorrhyncha populations.

DEVELOPED METHOD

The starting hypothesis for our analysis supposed independence of events both in space and time. The distribution of most species is not random, but we chose the Poisson distribution only as null hypothesis. Therefore, random data sets were generated as follows: The probability of n events in a small area dH is defined as:

$$P_n(dH) = \begin{array}{ll} 1 - dH \lambda & (n = 0) \\ dH \lambda & (n = 1) \\ 0 & (n > 1) \end{array}$$

For the whole area (H), this gives a Poisson distribution of $n(H)$ with a parameter (λ). Our null model was obtained from a series of PCAs performed on random data sets fulfilling the above conditions.

The data matrix includes the spatial distributions of a population at different points in time. The distributions are described by the relative frequencies among the patches, to decrease the strong effect of the increasing abundances resulting from the population dynamics. The other advantage of the relative data is that we can compare different data sets. The PCA of such a data matrix reflects the changes in spatial distribution.

PCA vectors reflect random noise as well as the real changes. To assess the effect of random noise on the evaluation, random data matrices with 5, 7, 10 and 15

observations (objects) at 3, 4, 6, 8, 10, 14, 20 and 28 sampling sites (variables) were generated. A PCA was performed on these matrices and the mean and S.D. of the % variance explained by the first principal component was interpreted as the main effect of random noise (Fig. 1). Both the number of variables and the number of objects influenced the quantity of the random noise, with the former having a larger effect. When the number of variables was fifteen or higher, the variance explained levelled out at 20–30%. In case of fewer variables, however, a sudden increase was found even when the number of objects were large. A decrease in the number of objects resulted in the decrease of the degrees of freedom in the correlation matrix. In parallel with this, the random noise and its standard deviation also increased. When exceeding ten, the effect of the number of objects is not substantial.

On the basis of this we chose random data matrices of ten objects and twenty-eight variables to study the relationships between the extent of spatial rearrangements and the percentage variance explained by the first PC vector. Different rearrangements were simulated between the first fourteen and second fourteen variables to construct a calibration curve to estimate the degree of rearrangements of real populations (Fig. 2). The shift occurred between the fifth and sixth objects. Data distributions were random at any given variable group of fourteen.

Three types of rearrangement were studied in which: (i) there was a complete shift, i.e. the two groups of objects had different variables (the second generation appeared in a new habitat type or left the old one); (ii) both groups of objects had the same variables (both generations occurred at both habitat types), but their ratio changed symmetrically; (iii) only one of the object groups (generations) showed a preference change between the two groups of variables (habitat types).

The rearrangement of simulated populations was checked on the separation of objects on the PCA scattergrams. The percentage variance belonging to the first principal component axis was related to the population segment performing habitat shift. The noise level at this matrix size was 20–24% (Fig. 1) and rearrangements inferior to this are masked (Fig. 2, below the broken line). This way a minimal

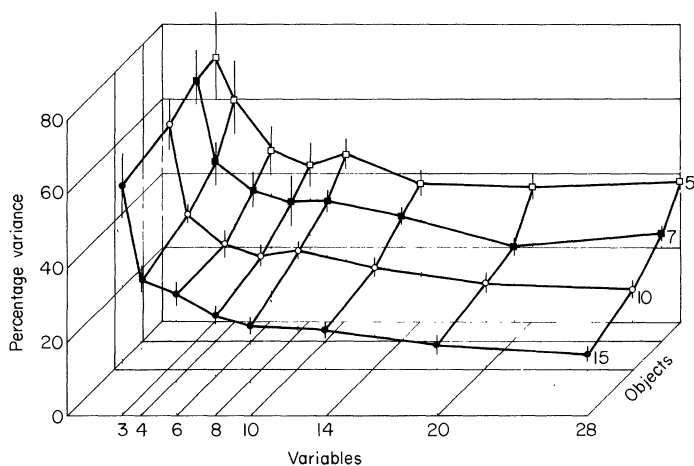


FIG. 1. Estimated levels of the 'noise' component (percentage variance associated with the first axis of the PCA from random data sets) in relation to sample size.

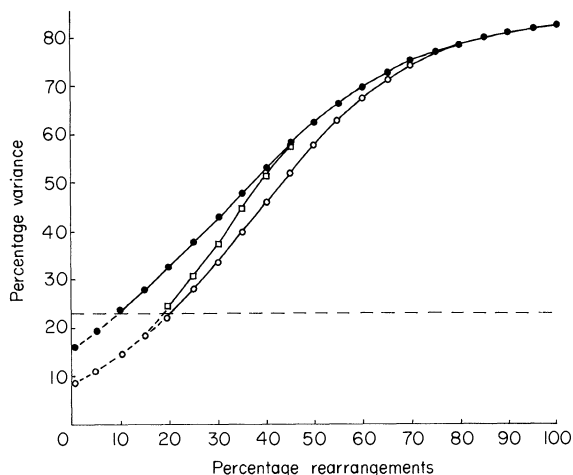


FIG. 2. Values of percentage variance explained by the first principal axis in the simulated rearrangements. Appearance at a new microhabitat (○), symmetric rearrangement (●), differential preferences during the season (□). Broken line indicates the 'noise' level.

detectable rearrangement of a population can be determined. When masked on the first, the rearrangement may be detected on the second or third axis.

APPLICATION OF THE METHOD TO SOME AUCHENORRHYNCHA POPULATIONS

Three conditions were applied to use of the method in the field: (i) presence of a patchy environment to ensure a wide scale of microhabitats; (ii) continuous sampling from the same patches; (iii) selection of suitable insects.

Study area

The study area was on a sandy grassland with sandhills and grooves in the Kiskunság National Park, Central Hungary. The difference in relief is rather small (some meters), but it causes considerable differences in microclimate and vegetation. In summer this region is very dry and hot, the average annual rainfall being 500 mm which falls mostly in spring.

A 2.4-ha part of the area was fenced off in 1976 to study secondary succession. The plant association on the sandhills of drier soil was *Festucetum vaginatae* Rapaics 1923 (names after Soó (1964)) with sparse cover. In the grooves, where the soil humidity was higher, *Molinio-Salicetum rosmarinifoliae* Soó 1933 association developed. About half of the study area was covered with *Potentillo-Festucetum pseudovinae* Soó 1939 association characteristic of the surrounding pasture. These associations were mosaically distributed with several transitions between each other (Fig. 3). Differences in relief (max. 250 cm) added to the mosaicity through moisture differences at different relief heights.

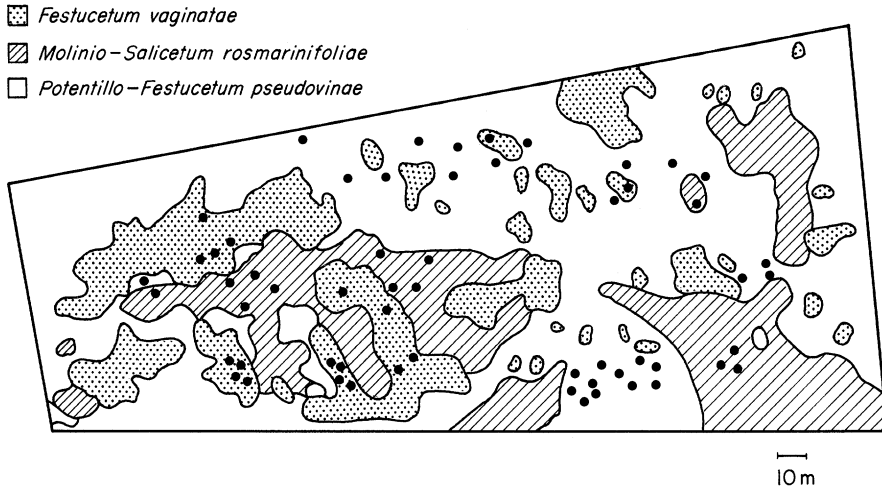


FIG. 3. Map of the study area. Nomenclature of the plant associations follows Soó (1964). Dots mark trap positions.

Collecting methods

The sampling method had to comply with the following requirements: (i) continuous sampling from the same site; and (ii) minimal disturbance of populations and habitat properties. Accordingly, pan traps (12 cm diameter), with ethylene-glycol as the killing and preserving agent, were operated at sixty sampling sites chosen in the different microhabitats (see Fig. 3) between April and November 1985. These microhabitats differed in relief, plant cover and plant species composition (Györffy & Kincsek 1988). Traps were emptied every 2 weeks.

Auchenorrhyncha species investigated

A total of 183 species of Auchenorrhyncha were collected on the site (Györffy 1987). To test the method developed, three species were chosen: *Turrutus socialis* (TS) (7799 individuals collected), *Mendrausus pauxillus* (MP) (1544 ind.) and *Kosswigianella exiqua* (KE) (6341 ind.). TS and KE showed a seasonal activity curve with two activity peaks which corresponded to two generations; MP showed two 'seasonal/activity generations' divided by a midsummer diapause (Schiemenz 1969a, b).

MP is a stenotopic, xerophilous species which hibernates in the egg stage, and is univoltine (Schiemenz 1969b). The previously recorded host-plant of MP is *Festuca sulcata* (Hackel) Nym. (Emeljanov 1964), but the area investigated is *Festuca pseudovina* Hackel ap. Wiesb. (Györffy & Kincsek 1988). There was a significant positive correlation between occurrence of MP and relative height of the trap position within the study area (relief); occurrence of TS did not show such an effect. TS occurs from xerophilous to hygrophilous biotopes. It hibernates in the egg stage, and has two generations per year (Schiemenz 1969b). The amount of plant cover had

a significant effect on TS but not on the other two species studied (Györfly & Kincsek 1988). TS was less specific in its host-plant choice. Negligible between-generation differences were found in microclimatic tolerances, in contrast to host-plant choices (Györfly & Kincsek 1988). KE lives only in xerophilous biotopes and hibernates in the larval stage (Schiemenz 1969a). Moving ability of KE is limited by its short wings (Ossiannilsson 1978). This species was closely associated with *Festuca vaginata* W. et K. in the area (Györfly & Kincsek 1988).

A further criterion in choosing the species was that they were collected from at least fifteen sampling sites, with a minimum of ten individuals in each trap. The following abbreviations are used to denote generations: juv1, first larval generation; juv2, second larval generation; ad1, first adult generation (or seasonal/activity generation); ad2, second adult generation.

RESULTS FROM FIELD DATA

Adults of all three species and larvae of TS showed bimodal seasonal activity (Fig. 4), and generations could easily be defined. Seasonal changes in the variance between traps, due to relative abundances, reflect changes in the spatial distribution (Fig. 4). This can be related to a habitat shift because clumping in favourable microhabitats increases the variance (e.g. TS juv1, 2, TS ad1, MP ad2). Another possibility is that the different microhabitat suitabilities become similar (e.g. the decrease in microclimatic differences during spring and autumn) when spatial distribution becomes more uniform. This was found for TS ad2 and KE juv1. In addition to these seasonal changes, the relationship between spatial distribution of the two generations is of interest, and can be calculated from the correlation coefficients of the relative abundances (Table 1).

High positive correlations were found between the spatial distributions of generations of the same species, indicating that rearrangements due to spatial rearrangements were small. The rearrangement between generations is inversely related to the correlation coefficient. From the detailed analysis, we conclude that the largest spatial rearrangement occurred between TS juv1 and juv2, while the smallest was between TS ad1 and ad2. However, the correlation matrix only indicated the phenomenon of habitat shift and not the segment of the population affected. This was studied by the pairwise PCA of the generations.

TABLE 1. Correlations between the spatial distribution of the generations studied. Levels of probability ($n = 60$) are as follows: $P < 0.1$ if $r > 0.21$; $P < 0.01$ if $r > 0.33$; $P < 0.001$ if $r > 0.41$

	KEad1	KEad2	KEjuv	TSad1	TSad2	TSjuv1	TSjuv2	Mpad1
KEad2	0.84	1						
KEjuv	0.88	0.81	1					
TSad1	-0.33	-0.26	-0.24	1				
TSad2	-0.33	-0.26	-0.24	0.94	1			
TSjuv1	-0.31	-0.25	-0.26	0.80	0.81	1		
TSjuv2	-0.34	-0.26	-0.24	0.88	0.88	0.71	1	
Mpad1	0.11	0.14	0.00	-0.16	-0.20	0.25	-0.23	1
Mpad2	0.07	0.03	-0.01	-0.14	-0.17	0.22	0.21	0.89

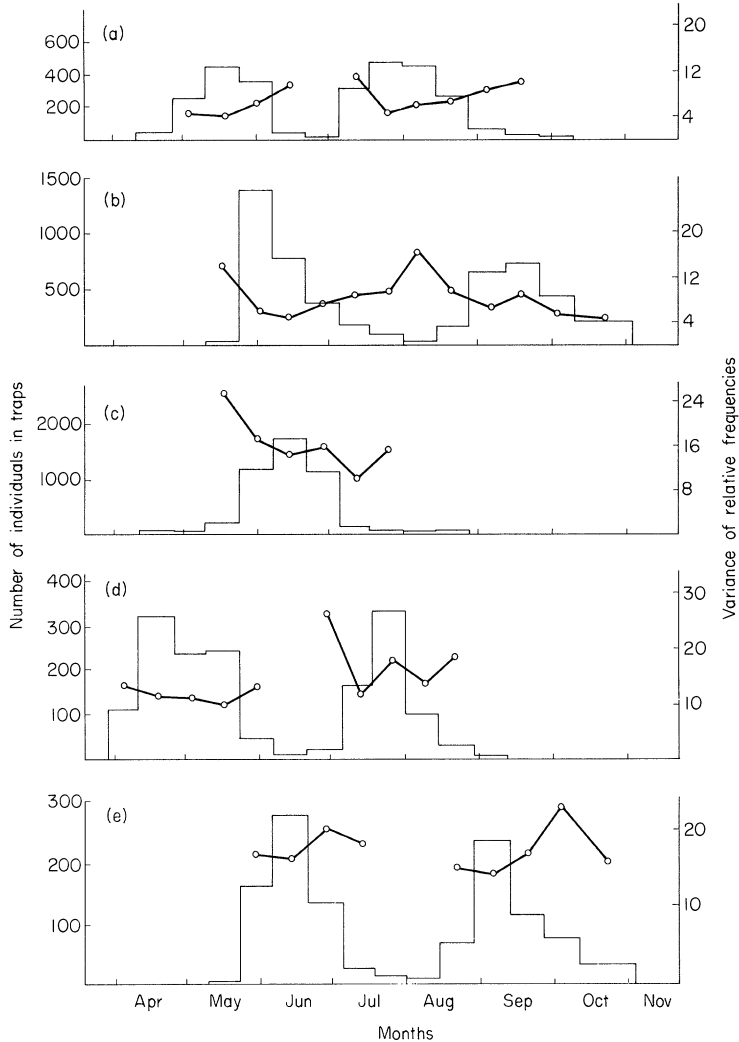


FIG. 4. Seasonal dynamics of species investigated based on the number of individuals and the variance of relative frequencies between traps (○): (a) TS larvae; (b) TS adults; (c) KE larvae; (d) KE adults; (e) MP adults.

Rearrangement between generations

In cases where rearrangements within generations exceed that between them, no between-generation shift can be detected. This was found for KE juv and KE ad1 (Fig. 5a), TS ad1–TS ad2 (Fig. 5b), or TS ad1–TS juv2 (Fig. 5c). In other cases, the rearrangement could be detected on the third axis: MP ad1–ad2 (Fig. 5d) and KE juv–KE ad2 (Fig. 5e), or on the second axis: KE ad1–ad2 (Fig. 5f). The rearrangement can be detected on the first axis only when the intergeneration shift is greater than the intrageneration one. This was small in some cases (TS juv2–ad2, Fig. 5g), large and significant in others (TS juv1–juv2, Fig. 5h; TS juv1–ad1,

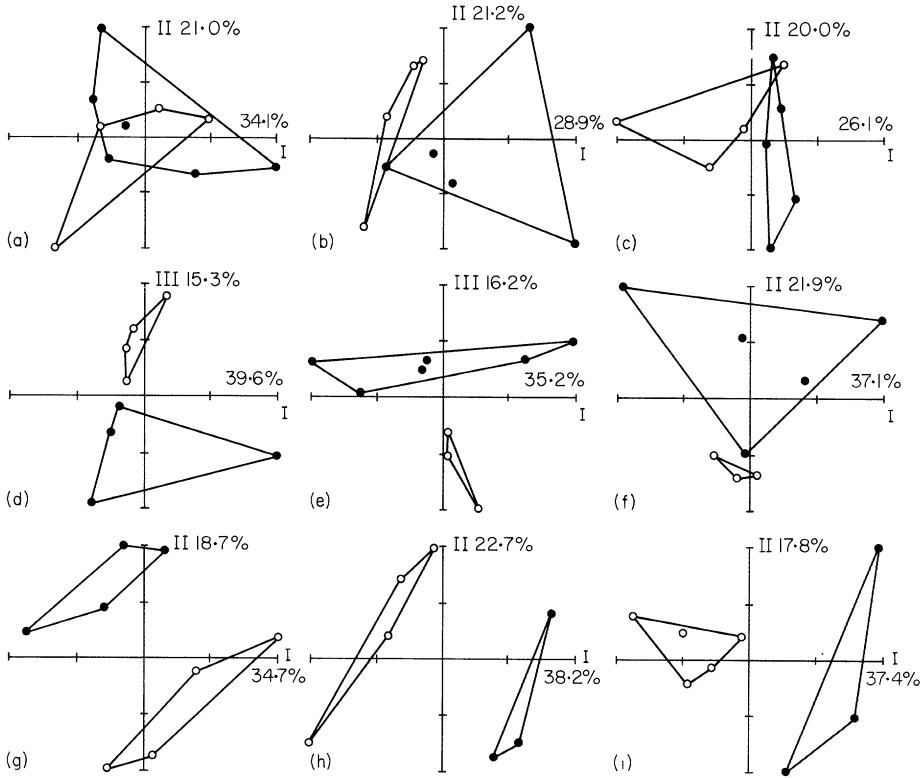


FIG. 5. Scatter diagrams obtained by pairwise comparisons by PCA between generations. Comparisons: (a) KE juv-ad1; (b) TS ad1-ad2; (c) TS ad1-juv2; (d) MP ad1-ad2; (e) KE juv-ad2; (f) KE ad1-ad2; (g) TS juv2-ad2; (h) TS juv1-juv2; (i) TS juv1-ad1; (●) the first, (○) the second member of the comparison.

Fig. 5i). In the last two cases, the extent of rearrangement can be described by the use of the calibration curve obtained by simulation. For TS juv1-ad1, this was 24–33%, for TS juv1-juv2, 25–34% of the generations changed habitat. All the other between-generation shifts detected by the scattergram were below the ‘noise threshold’.

Rearrangement within generation

More extensive within-generation spatial vagility is indicated when the pairwise PCA results in a first axis explaining variance above the noise threshold, but no difference can be detected between the generations or only on the second or third axis (Fig. 5d–f). Such a reaction was shown by MP, first phase generation, or KE ad1 and KE juv. The first principal axis explained 17.2, 9.3 and 5.8% variance above the noise threshold, respectively. In the case of TS, where intergeneration rearrangements were found, the differences between noise threshold and percentage variance of the first axis are insignificant, except TS ad2 where a certain degree of intragenerational rearrangement (6.9% above the noise threshold) was detected.

In all other comparisons, possible rearrangements are masked by random noise (Figs 1 and 2).

DISCUSSION

Simulation and its validity

Neutral models are fruitful approaches in the detection of 'fine-scale' phenomena by multivariate analysis (PCA). The variance of real data (e.g. from communities) is often loaded with a 'random noise' component (Gauch 1982). Special care is necessary with the results of PCA of small data matrix, as the increase in percentage variance is particularly pronounced (Stauffer, Garton & Steinhorst 1985). Our results with the PCA of simulated data matrices showed that this 'random noise' component is more sensitive to changes in the number of variables than in the number of objects. From these 'noise calibration curves' one can establish the optimal sizes of the matrices and the 'noise component' expected with given matrix sizes. Stauffer, Garton & Steinhorst (1985) analysing strongly asymmetric random and real data matrices showed that percentage variances for individual PCs were larger for real than for random data. However, field data matrices are often smaller and less asymmetric than the ones analysed by Stauffer, Garton & Steinhorst (1985). In such cases, random noise can mask real inter-relationships (Karr & Martin 1981), and this must be taken into account.

Our calibration curve was developed for the estimation of spatio-temporal pattern rearrangement between two groups of objects. Here two groups of variables could be separated, although these appear discontinuously and by gradual changes. This method can therefore be applied, in a slightly modified form, to study similar problems, e.g. rearrangements during succession and changes in feeding patterns.

Our model used the percentage variance explained by the first principal component. Here rearrangements greater than 22% can be detected. Changes less than this, if detectable from scattergrams, can be observed on the second or third principal axis (in the case of KE ad and MP ad). In theory, these can be measured in a similar way (Stauffer, Garton & Steinhorst 1985). However, the expected values are too small to have biological significance in this problem, so we did not consider it necessary to examine these axes.

Spatial rearrangement and its background

Tolerance limits towards the physical extremes are of basic importance in determining the distribution and abundance of populations, but interactions with other populations may further limit habitat width and decrease abundance (Fretwell & Lucas 1970; Connell 1975; Fraser & Size 1980). These pattern changes can be driven by changes in time of habitat suitability (Southwood 1962; Rauscher 1979; Taylor 1985; Delettre 1986; Marino 1986), habitat topography (Lewis 1969), microclimatic tolerances (Purcell 1976; Müller 1980, 1984), but can also be caused by the spatial separation of food resources or overwintering sites (Waloff 1973; Denno 1978; Denno, Douglas & Jacobs 1985) or ovipositing sites (Claridge & Wilson 1976; Tischler 1977; Rauscher 1979; McClure 1980; Denno 1985). The suitability of a given habitat changes in time (Rauscher 1979). If these changes in the quality and

quantity are similar in all resource patches, then diapause is a more profitable strategy to survive periods of resource unsuitability or unavailability. If, however, these changes are asynchronous, migration can have a higher adaptive value (Solbreck 1978; Roberts 1978; Denno *et al.* 1980).

Among the species studied, the strategy of MP was diapause. There was a rearrangement within subgenerations, which happened mostly before dormancy. This can be explained by some factors influencing the population dynamics. Although Auchenorrhyncha seem to resort more often to dormancy as a strategy to escape unfavourable conditions (Müller 1984), we focused on the non-random behavioural movements resulting in spatial rearrangement (Taylor 1986). In an area like our study site, dispersion is a necessity for species not diapausing; without it, local extinction could be very high (Roff 1974, 1975). This strategy is followed by TS. The distribution of the first larval generation, developing from the overwintering eggs, is less clumped than that of the summer generation. It is probable that TS ad1, tracking the shrinking microhabitats, laid eggs in these patches. One-third of the first adult generation changed its space compared with the larval stage developed in May. The next larval generation showed rearrangements within subgenerations, explained by the extreme midsummer climate. The effect of different developmental times are shown in the microhabitats: the milder autumn weather, released this environmental pressure and allowed a more even distribution of the TS ad2 generation.

Migration is usually towards more favourable habitat (in terms of food and environmental conditions) (Andrzejewska & Gyllenberg 1980). The presence of food-plants is significant for mono- and oligophagous species and, taking this into account, Nakasuji, Kimura & Nishida (1986) suggested a habitat and/or host-plant change hypothesis. When food becomes scarce or unsuitable, insect activity increases (Claridge, Reynolds & Wilson 1977; Thomas & Singer 1987): they migrate (Osborn 1932); Wilson, Heaton & Kennedy 1977) and macropterous morphs may even develop (May 1978).

Host-plant species of a polyphagous Auchenorrhyncha species can show different seasonal dynamics (Purcell 1976). In our study, TS has many probable host-plants, but KE and MP are more restricted in their hosts. A host-plant shift can be coupled with a rearrangement due to habitat shift. The mobile species are mostly polyphagous with a special nitrogen demand, while those which are less mobile are less specific in nitrogen demand but closely attached to their special host-plant (Prestidge & McNeill 1983). Rearrangements occurred either between (as in TS) or within (MP, KE) generations. These rearrangements are often not sharp and unequivocal because the migration effect is masked by a longer developmental time in the less favourable habitats.

The three species studied had different strategies to avoid unfavourable environmental conditions. KE is short-winged so its dispersal ability is limited and it is able to perform intrageneration rearrangements only. It is strongly monophagous and, although living in the plant association with the most extreme environmental conditions, does not become dormant. It follows that this species must possess wide tolerance limits. In this case, the intragenerational rearrangement may have arisen from differential mortality due to differing suitability of its habitats rather than from active dispersal. Monophagy, short wings and restricted distribution suggest that the adaptation is to certain patches, and not to the whole area. Therefore, the species does not take the risk of dispersal, but relies on its remarkable tolerance.

MP is also monophagous but it can go dormant, and did not show significant rearrangement. The species insists on the microhabitats and prefers the *Festuca pseudovina* plant. Its adaptive strategy is dormancy, thus overcoming unfavourable conditions passively.

TS is polyphagous and has wide ecological tolerance limits (Schiemenz 1969a, b). Its more flexible resource utilization is reflected by its vagility, with its distribution limited by plant cover and probably by nitrogen level (Prestidge & McNeill 1983). This species can better utilize the patchy habitat because it is more adapted to the habitat than to the patches. The 'large-scale' trend, suggesting that species with wide distribution are generally abundant but have wider population fluctuations than species with more restricted distribution and resource use (Gaston & Lawton 1988), seems to be true at the microhabitat scale also.

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