Resource partitioning in Finnish woodpeckers

RISTO ALATALO

ALATALO, R. H. 1978: *Resource partitioning in Finnish woodpeckers.* — Ornis Fennica 55:49—59.

The resource partitioning of the four most abundant woodpeckers in southern Finland *(Picus canus, Dendrocopos major, D. minor,* and *Dryocopus martius)* is analysed by a multivariate method called the components of diversity method. One-dimensional partition of diversity gives the following decreasing order of importance for resource-utilization axes: habitat, tree species or substrate, foraging technique, region (area), condition of tree, relative height in tree, portion of tree. A three-dimensional partition of diversity is made for the most important axes. All the species pairs are segregated more than 33 % by these resource-utilization axes. Since the association between these three axes is high and variable, one-dimensional methods do not measure resource partitioning reliably. *Dendrocopos major* has the broadest niche along the habitat and technique axis, while *D. minor* and *Dryocopus martius* are habitat specialists, which accords with previous knowledge.

Risto Alatalo, Department of Genetics, University of Oulu, Postilokero 191, SF-90101 Oulu 10, Finland

Introduction

In recent studies of community structure, much use has been made of the concepts of niche breadth and overlap (see CODY 1974, PIANKA 1974, for reviews). The most useful approach to these complex phenomena seems to be to analyse subcommunities or guilds (e.g. SCHOENER 1968, PIANKA 1973, HEED et al. 1976, HERRERA & HIRALDO 1976). Woodpeckers form a guild *(sensu* ROOT 1967, p. 335) of insectivorous birds capable of undersurface feeding and this guild is particularly suitable for the measurement of resource-utilization, because foraging sites in trees are relatively easy to classify.

Finnish woodpeckers are resident or wandering species which occur all the year round almost sympatrically. It is therefore possible to make observations throughout the year. This is important for the study of resource partitioning; erroneous conclusions may be made if populations are studied only in the breeding season (BAKER & BAKER 1973).

The concept of niche used in this analysis of a Finnish woodpecker community is the frequency distribution of occurrence along resource-utilization axes, though this is not compatible with the so-called Hutchinsonian niche (see SCHOENER 1974, WHITTAKER & LEVIN 1975). The measurement of niche breadth and overlap in a system of many interdependent resource-utilization axes requires an appropriate multivariate method. Several interdependent variables can be considered simultaneously by multivariate methods (see JOLICOEUR 1959, for an example). Using the components of diversity method (Alatalo & Alatalo 1977), I estimated the contributions due to many axes both simultaneously and exclusively. This paper, together with others in preparation, represents the first empirical application of the multivariate partition of diversity.

Components of diversity are used to estimate overlaps between species with respect to various niche and habitat axes. Interactions between axes are estimated at the same time. Diversity is also used in the estimation of niche breadth and habitat selection.

The niches of the four most abundant woodpecker species in southern Finland are analysed: the Grey-headed Woodpecker *Picus canus*, Great Spotted Woodpecker *Dendrocopos major*, Lesser Spotted Woodpecker *Dendrocopos minor* and Black Woodpecker *Dryocopus martius*. Other woodpecker species are too rare for this kind of analysis, and they have been omitted.

Methods

Observations were made in three regions in S Finland (60° through 62°N) by the following ornithologists: 1) Eura-Karinainen (Tuomo Hurme, Antti Karlin), 2) Karkkila (Kari Virta, Kari Degerstedt, Hannu Friman, Heikki Luoto, Kalle Virta), and 3) SE Finland (Ismo Hölsä, Teemu Leino, Seppo Löfgren, Harri Makkonen, Anssi Muurikka). The number of observations is nearly evenly distributed among these three regions (Table 5).

Most observations were made during the non-breeding season, the proportion of observations made in May-June being low for each species: *canus* 12 %, *major* 8 %, *minor* 18 % and *martius* 7 %. Preliminary observations had been made during the years 1973—74 and analysed by univariate methods (Alatalo 1975). More detailed observations for this paper were made during the years 1975—76. Each woodpecker observation contained information on the following variables: date of observation, commune (region), tree species or other substrate, relative height in tree, condition of tree, tree portion, foraging technique, and habitat (with two independent classifications). "First sighting" records are used instead of continuous observation of single individuals. A problem with this method is the variation in the conspicuousness of woodpeckers between sites, but the observations are independent of each other (Schoener & Schoener 1971, Alerstam et al. 1974, Ulfstrand 1976).

Unfortunately, the sampling method is non-random, because the ornithologists made their observations without any definied counting transects or areas representative of each region, but bias due to non-random sampling does not invalidate some interspecific comparisons. However, the results should be regarded as preliminary and many ecological problems involving ecological segregation among Finnish woodpeckers still await more exact and extensive field work.

Classification was reorganized by combining related categories with few observations in order to lower bias due to small samples in each cell of the multi-dimensional resource matrix (Table 1). Many observations which were classified as non-foraging concern woodpeckers looking for a suitable foraging site with prey and were therefore included in the calculations. On the other hand, woodpeckers are usually seen in their normal habitat and microhabitat, and most observations give some information about the ecology of the species studied. Similar lumping of "first sightings" was used by Schoener & Schoener (1971) for *Anolis* lizards, with encouraging results. In woodpeckers, the number of non-foraging observations was high for *canus* and *martius* (Table 4).

The principle of the components of diversity method is described by Alatalo & Alatalo (1977). The so-called Basharin correction is used in estimating H', Shannon's entropy or diversity index (cf. Hutcheson 1970). For better interpretation of results and meaningful interactions, the antilogarithmic index exp(H') was used. The details of notation used in this paper are available on request.

Interpretation of components

The component of species diversity contributed by between-cell variation in species composition is V_{BPT}. This measures the extent to which we find ecological differences between species when we use their utilization distribution with respect to habitat, tree and technique simultaneously.

The component of species diversity accounted for by different species com-

TABLE 1. Categories of resource-utilization axes used for partition of diversity. The term 'non-wild' refers to a bird-feeding site, park, garden, or patch of wood surrounded by fields.

Axis	Categories
Habitat	Pine forest, non-wild pine wood, spruce forest, non-wild spruce wood, alder forest or wood, other deciduous forests, non-wild deciduous forests, other habitats (not woods).
Tree	Pine, spruce, birch, alder, other trees, other substrate, bird-feeding site.
Technique	Pecking, tearing, gleaning, cones, bird-feeding site, other foraging, apparently not foraging.
Region	Eura and Karinainen, Karkkila, Southeastern Finland (Savitaipale, Ylämaa, Savonlinna, Lappeenranta, Miehikkälä).
Condition	Live tree, stunted tree, dead tree, not tree.
Height	Lowest quarter, second quarter, third quarter, highest quarter, not tree.
Portion	Trunk, branch or twig, not tree.

position in each habitat is V_B. This between-habitat component of species diversity is an example of between-category components. A two-dimensional between-category component of species diversity is, for example, V_{BP}, the component due to distribution of species on the habitat and tree axes considered simultaneously.

The exclusive between-habitat component of species diversity, $V_{B/PT}$, which is independent of tree and technique, measures the average extent to which species are segregated by habitat in each tree × technique category. The exclusive between-habitat × tree component of species diversity $V_{BP/T}$, which is independent of technique, measures the extent to which species are segregated by simultaneous use of habitat and tree categories for each technique.

The interaction habitat × tree component of species diversity is R_{BxP}, which gives positive values when habitat and tree segregate species correlatively (redundantly). The negative interaction is due to segregation of species by the two-dimensional categories habitat × tree when these differences between species cannot be found completely by one-dimensional use of habitat and tree axes. The second-order interaction habitat × tree × technique in the three-dimensional segregation of species by habitat, tree and technique axes is R_{BxPxT}.

Associations between resource-utilization axes can be estimated for each species and for pooled species when the ability of axes to separate species is not considered but rather individuals are considered. Thus components of diversity can be determined for each resource axis. Resource-utilization diversities can be used as a measure of niche breadth, e.g. habitat diversity $D(B)_{\cdot\cdot}$ measures niche breadth along the habitat axis.

The interaction tree × technique component of habitat diversity, $R(B)_{PxT}$, measures the extent to which tree and technique axes are associated in their ability to determine habitat for a woodpecker. Resource diversities for other axes are calculated and partitioned in a similar way to that used for habitat.

One-dimensional components of diversity

The habitat axis segregates *major,* which is frequent in pine forests, while the other species are concentrated in deciduous forests (Table 2). Non-wild spruce forests are favoured by *canus.* Consequently, *major* uses pines frequently and the other species birches (Table 3). Typical techniques are bird-feeding sites in *canus* (this is overestimated by collection of observations because occurrences at bird-feeding sites are readily seen), cones in *major*, pecking in *minor*, and tearing and pecking in *martius* (Table 4). Geographically, *major* seems to be common throughout the region, *canus* in Karkkila and SE Finland (due to some wintering at a bird-feeding site), *minor* in Karkkila, and *martius* in Karkkila and Eura-Karinainen (Table 5). However, this result should not be used for estimating geographical occurrence. Besides being frequently observed in live trees, *canus* is often seen on substrates other than trees (bird-feeding site), *minor* in dead trees, and *martius* in stunted trees (Table 6). Along the height axis, *minor* and *major* are often high in trees, while *martius* is mainly lower (Table 7). Typically, *canus* is not

Table 2. Resource-utilization distributions along habitat axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Pine-dominated forest	0.028	0.274	0.023	0.130	0.193
Non-wild pine wood	0.055	0.089	0.006	0.014	0.063
Spruce-dominated forest	0.037	0.087	0.018	0.065	0.069
Non-wild spruce wood	0.284	0.131	0.000	0.007	0.110
Deciduous forest	0.330	0.114	0.596	0.536	0.262
Non-wild deciduous wood	0.165	0.169	0.088	0.051	0.141
Alder forest or wood	0.046	0.086	0.146	0.188	0.106
Other habitats	0.055	0.048	0.123	0.007	0.055
Number of observations	109	687	171	138	1105

Table 3. Resource-utilization distributions along tree axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Pine	0.110	0.349	0.023	0.188	0.255
Spruce	0.055	0.068	0.012	0.065	0.058
Birch	0.358	0.194	0.550	0.522	0.306
Alder	0.064	0.048	0.111	0.101	0.066
Other trees	0.064	0.121	0.234	0.029	0.121
Other substrate	0.193	0.125	0.023	0.094	0.112
Bird-feeding site	0.156	0.095	0.047	0.000	0.081

Table 4. Resource-utilization distributions along technique axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Pecking	0.055	0.087	0.322	0.188	0.133
Tearing	0.064	0.052	0.058	0.217	0.075
Gleaning	0.083	0.135	0.146	0.101	0.128
Cones	0.000	0.290	0.000	0.000	0.180
Bird-feeding site	0.183	0.093	0.047	0.000	0.083
Other foraging	0.018	0.013	0.006	0.043	0.016
Apparently not foraging	0.596	0.329	0.421	0.449	0.385

concentrated in any special height category. With regard to tree portion, *martius* is the most specialized on trunks (Table 8).

According to BLUME (1971, p. 5), these species form the following array, from *Bodenspechte* to *Hackspechte: canus, martius, major, minor.* Ground-feeding is underestimated in my data because the conspicuousness of woodpeckers is poor when they are on the ground. Thus my results do not lend strong support to this array, but it seems to be in accord with the findings that *minor* and *major* are frequently high in the tree. Testing of the array would require a suitable sample from feeding sites.

The ability of resource-utilization axes to segregate species is measured by main effects or between-category components in Table 9. The four species of woodpeckers are mostly segregated by habitat and tree. Between-category diversities are the greatest for these axes and I consider them to be

TABLE 5. Resource-utilization distributions along region axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Eura and Karinainen	0.128	0.303	0.181	0.341	0.271
Karkkila	0.431	0.265	0.608	0.601	0.376
SE Finland	0.440	0.432	0.211	0.058	0.352

TABLE 6. Resource-utilization distributions along condition axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Live tree	0.385	0.486	0.380	0.377	0.446
Stunted tree	0.101	0.189	0.199	0.362	0.204
Dead tree	0.156	0.124	0.351	0.188	0.170
Non-tree substrate	0.358	0.201	0.070	0.072	0.180

TABLE 7. Resource-utilization distributions along height axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Lowest quarter	0.202	0.082	0.135	0.181	0.114
Second quarter	0.138	0.138	0.146	0.319	0.162
Third quarter	0.128	0.256	0.246	0.297	0.247
Highest quarter	0.229	0.365	0.404	0.159	0.332
Not tree, without height	0.303	0.159	0.070	0.043	0.145

TABLE 8. Resource-utilization distributions along portion axis.

Category	*canus*	*major*	*minor*	*martius*	Pooled
Trunk	0.459	0.524	0.591	0.790	0.561
Branch or twig	0.147	0.265	0.327	0.109	0.243
Not tree, without portion	0.394	0.211	0.082	0.101	0.195

TABLE 9. Main effects for resource-utilization axes. $\overline{D}$ = average overlap between woodpecker species along axis. V = segregation of woodpecker species by axis measured as effective number of species exp(H') and percentage (%) of the maximal segregation. Pooled diversity exp(H') is 2.93 (N = 1105).

Axis	$\overline{D}$	V	%
Habitat	2.57	0.35	18.3
Tree	2.71	0.22	11.2
Technique	2.74	0.19	9.7
Region	2.80	0.13	6.6
Condition	2.82	0.11	5.7
Height	2.83	0.10	5.1
Portion	2.84	0.08	4.3

the most important axes. Portion, height, condition, and region have relatively little ability to segregate these species.

The main effects are relatively low and axes must be used simultaneously to find a better segregation for the species. The three axes with the highest between-category diversities were selected for multivariate analysis. The sample size seems to be sufficient for a three-dimensional partition of diversity. To increase the number of dimensions requires an increase in sample size proportional to the increase in the number of cells in the resource matrix. E.g. if height were taken as the fourth dimension for multivariate analysis, we should require approximately five times the number of observations available.

Three-dimensional components of diversity

Table 10 presents a three-dimensional partition of diversity for the axes which have the strongest main effects: habitat, tree and technique. Between-technique diversity V_T is 9.7 %, but owing to the negative interaction, exclusive between-technique diversity $V_{T/BP}$ is 14.9 %. Two-dimensional segregation of the species is most efficient when habitat and technique are used, though the tree has a greater main effect than technique. The reason for this is the redundancy between habitat and tree, R_{BxP} = 2.0 %, and the negative interaction habitat × technique, R_{BxT} = —2.1 %.

For interpretation of segregation between species pairs, the 30 % between-category component is arbitrarily chosen to signify that species are ecologically distinct. This is more than is required for a statistically significant difference, but statistical significance does not measure ecological importance.

For *canus-major* all three axes are required to obtain segregation over 30 %. These species are nearly segregated by simultaneous use of habitat and technique for each tree, $V_{BT/P}$ = 29.5 %. Negative interactions are typical of *canus-major*, which underlines the need to use axes simultaneously.

Together, habitat and tree segregate *canus-minor*, V_{BP} = 43.3 %, and the two species are nearly segregated one-dimensionally by habitat. This pair of species is characterized by positive interaction between technique and the other dimensions, which indicates that segregation due to technique correlates with segregation along the habitat and tree axes. Frequent use of the birch and "other tree" category segregates *minor* from *canus* slightly on the tree axis, since the latter uses "other substrates" and bird-feeding sites more often.

Habitat nearly segregates *canus-martius*, and they are clearly segregated two-dimensionally by habitat and tree (V_{BP} = 41.9 %) or habitat and

TABLE 10. Three-dimensional partition of diversity for woodpecker species by habitat (B), tree (P), and technique (T). $D_{\dots}$ is total diversity of species considered. V_A measures how much species are segregated by axis A. R is an estimate of the interaction between the axes indicated by subscripts. It measures the extent to which axes separate species redundantly. Components of diversity are given as a percentage of the theoretical maximum.

	Four species	Components for species pairs *canus major*	*canus minor*	*canus martius*	*major minor*	*major martius*	*minor martius*
$D_{\dots}$	2.93	1.49	1.95	1.99	1.65	1.57	1.99
V_{BPT}	42.4	33.0	50.9	55.6	49.0	41.9	41.1
V_{B}	18.3	8.0	25.3	27.3	28.1	18.4	9.2
V_{P}	11.2	3.5	19.3	11.9	17.2	9.4	18.5
V_{T}	9.7	8.1	12.3	17.2	12.8	14.2	9.1
V_{BP}	27.5	17.1	43.3	41.9	36.3	23.8	23.5
V_{BT}	30.1	20.9	29.4	41.9	38.7	36.6	21.2
V_{PT}	23.8	16.6	26.3	24.7	30.5	23.6	32.3
$V_{B/PT}$	18.7	16.4	24.6	30.9	18.5	18.3	8.8
$V_{P/BT}$	12.4	12.1	21.4	13.7	10.3	5.3	19.9
$V_{T/BP}$	14.9	15.9	7.5	13.7	12.7	18.1	17.5
$V_{BP/T}$	32.7	25.0	38.6	38.4	36.2	27.7	31.9
$V_{BT/P}$	31.2	29.5	31.6	43.7	31.8	32.5	22.6
V_{PxT}	24.1	25.0	25.6	28.3	20.9	23.5	31.8
R_{BxP}	2.0	—5.6	1.2	—2.7	9.0	4.0	4.2
$R_{PT/B}$	—2.1	—4.9	8.1	2.6	2.2	—4.0	—2.8
R_{BxT}	—2.9	—5.1	5.3	4.4	—0.5	0.0	—4.6
R_{BxPxT}	0.2	—2.1	8.6	3.4	1.6	—0.1	1.0

technique (V_{BT} = 41.9 %). Habitat in each two-dimensional category tree × technique segregates *canus-martius* ($V_{B/PT}$ = 30.6 %). Strong two-dimensional segregation of these species is afforded by the simultaneous use of habitat and technique in each tree category ($V_{BT/P}$ = 43.7 %). Positive interaction tree × technique for *canus-martius* lowers segregation by these axes when they are used together.

Habitat nearly segregates *major-minor,* and they are segregated two-dimensionally by habitat and technique (V_{BT} = 38.7 %). Habitat × tree gives a high positive interaction for *major-minor,* the former being frequent on pines in pine forests and the latter on birches in deciduous forests.

For *major-martius* habitat and technique give two-dimensional segregation (V_{BT}' = 36.6 %), which is strengthened by negative interaction, R_{BxT}. Positive interaction habitat × tree lowers the simultaneous segregation by these axes for *major-martius.*

Tree and technique give two-dimensional segregation for *minor-martius* (V_{PT} = 32.3 %). Habitat and tree give segregation for these species if they are used simultaneously in each technique ($V_{PB/T}$ = 31.9 %). The interaction habitat × tree is also positive for *minor-martius,* but the interaction tree × technique is negative for them.

Characteristically, all pairs of species are segregated two-dimensionally more than 30 %, except *canus-major,* which are segregated three-dimensionally, i.e. information on all three axes is needed to interpret this ecological segregation. The interaction components are negative for this pair of species, indicating that they have a different foraging pattern in each tree and select a tree differently in each habitat.

The interaction components vary greatly: five being more negative than —4 % and seven more positive than +4 %. This indicates that independent use of many dimensions with summation or multiplication to combine the information from different axes is an unrealistic approach to this kind of data. Variation in the associations between axes makes one-dimensional methods unreliable for measurement of resource partitioning.

The two-dimensional segregations usually include the habitat axis, an exception being *minor-martius*, which are segregated by tree and technique.

Interaction components of niche breadth

The associations between the resource-utilization axes were measured by their interactions, which are 14 through 16 per cent for the pooled species (Table 11). In *canus* interactions are great, in *minor* and *martius* they are small. Frequent use of a bird-feeding site is the main reason for the high interaction in *canus*. The bird-feeding site has its own category in both the tree and technique axes and was situated in a non-wild spruce wood.

D. major seems to have the broadest niche. *P. canus* has the narrowest niche along the technique axis. The habitat and tree axes give the narrowest niche for *minor*.

The interaction components are dependent on each other, but this problem will be discussed in a further paper. The interaction components for habitat, tree and technique diversities indicate between-species variation in the association between resource-utilization axes. This is a good reason to recommend the use of multivariate methods in the measurement of resource partitioning. As indicated earlier, the axes were interdependent in their ability to segregate species. They are also dependent on each other as niche axes of a species and pooled species.

TABLE 11. Niche breadth and interaction between resource-utilization axes. The number of observations is *N*. $\mathrm{D(B)}_{\cdot\cdot}$ is niche breadth along the habitat axis. $\mathrm{R(B)}_{\mathrm{PxT}}$ is a measure of the dependence between tree and technique in their ability to determine habitat for the woodpecker. Niche breadth along tree (P) and technique (T) and their interaction components are indicated analogously.

	Species Pooled	*canus*	*major*	*minor*	*martius*
N	1105	109	687	171	138
$\mathrm{D(B)}_{\cdot\cdot}$	7.01	5.67	7.11	3.55	4.07
$\mathrm{D(P)}_{\cdot\cdot}$	5.83	5.80	5.80	3.68	4.09
$\mathrm{D(T)}_{\cdot\cdot}$	5.36	3.52	5.18	3.92	4.01
$\mathrm{R(B)}_{\mathrm{PxT}}$	14.2	20.0	10.4	7.3	5.4
$\mathrm{R(P)}_{\mathrm{BxT}}$	15.7	20.2	15.2	7.5	2.6
$\mathrm{R(T)}_{\mathrm{BxP}}$	14.4	22.1	14.5	1.9	9.4

Discussion

Resource partitioning in ecological communities or guilds generally appears to segregate species multidimensionally (SCHOENER 1974); hence a multivariate method possesses the statistical properties required to do justice to this complex phenomenon. The negative interaction for *canus-major* means that these species are segregated more effectively by using a multidimensional measurement. Most of the pairs of species are segregated two-dimensionally, if a between-category component exceeding 30 % is interpreted as effective segregation. The association between resource-utilization axes varies between species in woodpeckers and this is another reason for using multivariate methods to measure resource partitioning. Since the interaction components are variable, multidimensional overlap indices calculated with the products or sums of one-dimensional indices are unreliable (see MAY 1975).

There are several methods for measuring association in a multiway contingency table (see BISHOP et al. 1975), but components of diversity provide a convenient ecological interpretation (ALATALO & ALATALO 1977). The use of a standard method has many advantages; when different methods are employed the same data can be used to support divergent postulates (e.g. JUMARS 1974).

Components of diversity are calculated for discrete axes. Since many difficulties arise when both continuous and discrete axes are used (see BISHOP et al. 1975), the continuous axes were transformed to discrete ones by artificial classification (e.g. relative height categories). The problems of scaling involved in determining suitable categories for axes have been discussed by CODY (1974). Here an attempt was made to select objective categories, so that observations made by different persons might be comparable. Simple classifications were therefore used, but at the same time the ecological differences between species are underestimated. Niche measurements are affected by the sampling method chosen, e.g. the range of communities included and the representation of particular communities (WHITTAKER & LEVIN 1975).

According to SCHOENER (1974), the most critical problem in applying models of competition is the identification of resources in nature. He suggested the use of statistical techniques such as discriminant (GREEN 1971) or multiway-contingency-table analysis (FIENBERG 1970) to determine what axes and categories best separate consumer niches. Discriminant analysis requires continuous axes, and hence its usefulness for measurement of resource partitioning is limited (e.g. we cannot measure tree species on a continuous scale). Multiway-contingency-table analysis has been used by M'CLOSKEY (1975) to analyse habitat selection in a rodent species, and by SCHOENER & SCHOENER (1971) for niche analysis of an *Anolis* lizard community. Multivariate components of diversity are easier to calculate and seem to be easier to interpret than the multiway-contingency-table analyses by partitioning chi-square. A basic difference between these methods is that components of diversity *measure* associations and segregations whereas the chi-square only *tests* them. The partition of diversity can be used when the measurement of interactions and overlaps is preferred to testing.

Habitat seems to be the most important resource axis in woodpeckers. However, it is not possible to decide in this study whether this is due to true habitat *selection* or a habitat *correlation* resulting from some external agent responsible for interspecific differences in distribution (WIENS 1976). The tree also seems to be an important axis in woodpeckers and is a kind of measure of microhabitat. The partitioning of resources in birds can be estimated from microhabitat distribution and behaviour (BAKER & BAKER 1973). The technique axis, which measures behaviour seems to be an important axis in woodpeckers in addition to habitat and microhabitat distribution. The negative interaction between habitat and technique strengthens the importance of technique in multivariate measurement, while the positive interaction between habitat and tree indicates that they are redundant axes. Stomach analyses are one possible way of measuring resource partitioning, but alone they probably overestimate overlap between species (ORIANS & HORN 1969, BAKER & BAKER 1973). However, the simultaneous use of microhabitat distribution, foraging behaviour and stomach analyses is difficult (PIANKA 1976).

The number of coexisting species is supposed to be determined by the pattern of niche overlap, and hence the amount of niche overlap should be proportional to the intensity of competition (LEVINS et al. 1973, PIANKA 1974). However, niche overlap is neither a necessary nor a sufficient condition of interspecific competition, although it is a necessary but not a sufficient condition of exploitation competition (PIANKA 1976). Spatial overlap often measures postcompetitive situations and overlap values may not equal competition coefficients (SCHRODER & ROSENZWEIG 1975, RATCHKE 1976, SEIFERT & SEIFERT 1976). An extensive realized niche overlap may actually be connected with reduced competition (PIANKA 1974, HERRERA & HIRALDO 1976, CONNER & ADKISSON 1977). This suggestion is an attractive one, since the lowest overlap in this study is for *canus-martius*, a pair of species which may actually compete in nature (see HAILA & JÄRVINEN 1977). This segregation may be due to active avoidance, if *martius* can outcompete *canus*.

Resource partitioning is affected by social dominance (MORSE 1974) and this phenomenon would be an interesting subject for future research. Seasonal variation and regional differences in resource partitioning may be important, but to explore these aspects more field data are needed. In addition to extensive field work, the refinement of observation methods and axis classification is also necessary.

Acknowledgements. This work has been supported by a grant from the Emil Aaltonen Foundation. I wish to thank everyone who has taken part in the field work (see Methods). Phil. Lic. Rauno Alatalo has helped with statistical analysis of the data. I thank Dr. S. Sulkava and Professor E. Pulliainen for reading an earlier draft of the manuscript.

Selostus: **Neljän tikkalajin elin- ja ruokailupaikan valinnasta Etelä-Suomessa**

Neljän tikkalajin (harmaapäätikka, käpytikka, pikkutikka ja palokärki) havainnoista kerättiin tiedot: 1) kunta (alue), 2) biotooppi, 3) puulaji, 4) puun laatu (elävä, kituva, kuollut), 5) suhteellinen korkeus puussa, 6) puun osa (runko, oksisto) ja 7) ruokailutekniikka (taul. 1). Kunkin lajin havainnoista yli 80 % oli pesintäkauden ulkopuolelta. Käpytikka oli usein mäntymetsässä muiden lajien keskittyessä lehtimetsiin (taul. 2). Harmaapäätikka oli usein asutuksen lähellä kuusikossa. Käpytikka oli usein männyssä ja muut lajit koivussa (taul. 3). Harmaapäätikka ruokaili usein lintulaudalla, käpytikka käytti käpyjä, pikkutikka hakkasi usein ja palokärki repi ja hakkasi (taul. 4). Harmaapäätikkahavaintoja tuli runsaasti Karkkilasta ja Kaakkois-Suomesta, lisäksi Karkkilasta oli eniten pikkutikka- ja palokärkihavaintoja, vaikka palokärki on yleinen myös Eura-Karinainen -alueen havainnoissa (taul. 5). Pikkutikka ja käpytikka olivat usein korkealla puussa, palokärki taas matalalla (taul. 7) sekä rungolla (taul. 8). Biotooppi ja puulaji erottelivat lajit parhaiten (V ja %, taul. 9). Ne mittaavat osittain samaa lajien välistä eroa, mutta biotooppi ja tekniikka erottelivat lajeja tehokkaammin yhdessä kuin erikseen. Suurin ero saatiin harmaapäätikan ja palokärjen välille. Käpytikan biotooppivalikoima ja ruokailutekniikka oli monipuolisin, kun taas pikkutikka ja palokärki olivat selvimmin erikoistuneet biotoopin valinnassaan.

References

Alatalo, R. H. 1975: Tikkojen Picinae ekologisista eroista. Manuscript, Dept. Zoology, Univ. Oulu.

Alatalo, R. V. & R. H. Alatalo 1977: Components of diversity: Multivariate analysis with interaction. — Ecology 58:900—906.

Alerstam, T., S. G. Nilsson & S. Ulfstrand 1974: Niche differentiation during winter in woodland birds in southern Sweden and the island of Gotland. — Oikos 25:321—330.

Baker, M. C. & A. E. M. Baker 1973: Niche relationships among six species of shorebirds on their wintering and breeding ranges. — Ecol. Monogr. 43:193—212.

Bishop, Y. M. M., S. E. Fienberg & P. W. Holland 1975: Discrete multivariate analysis. — Cambridge, Mass.

Blume, D. 1971: Spechte fremder Länder. — Neue Brehm-Bücherei 434, Wittenberg Lutherstadt.

Cody, M. L. 1974: Competition and the structure of bird communities. — Princeton, N. J.

Conner, R. N. & C. S. Adkisson 1977: Principal coponent analysis of woodpecker nesting habitat. — Wilson Bull. 89:122—129.

Fienberg, S. E. 1970: The analysis of multidimensional contingency tables. — Ecology 51:419—433.

Green, R. H. 1971: A multivariate statistical approach to the Hutchinsonian niche: Bivalve molluscs of central Canada. — Ecology 52:543—556.

Haila, Y. & O. Järvinen 1977: Competition and habitat selection in two large woodpeckers. — Ornis Fennica 54:73—78.

Heed, W.B., W. T. Starmer, M. Miranda, M.W. Miller & H. J. Phaff 1976: An analysis of the yeast flora associated with cactiphilic Drosophila and their host plants in the Sonoran Desert and its relation to temperate and tropical associations. — Ecology 57:151—160.

Herrera, C. M. & F. Hiraldo 1976: Food-niche and trophic relationships among European owls. — Ornis Scand. 7:29—41.

Hutcheson, K. 1970: A test for comparing diversities based on the Shannon formula. — J. theor. Biol. 29:151—154.

Jolicoeur, P. 1959: Multivariate geographical variation in the wolf Canis lupus L. — Evolution 13:283—299.

Jumars, P. A. 1974: Two pitfalls in comparing communities of differing diversities. — Amer. Natur. 108:389—391.

Levins, R., M. L. Pressick & H. Heatwole 1973: Coexistence patterns in insular ants. — Amer. Scient. 61:463—472.

M'Closkey, R. T. 1975: Habitat dimensions of white-footed mice, Peromyscus leucopus. — Am. Midl. Nat. 93:158—167.

May, R. M. 1975: Some notes on estimating the competition matrix, α. — Ecology 56: 737—741.

Morse, D. H. 1974: Niche breadth as a function of social dominance. — Amer. Natur. 108:818—830.

Orians, G. H. & H. S. Horn 1969: Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. — Ecology 50:930—938.

Pianka, E. R. 1973: The structure of lizard communities. — Ann. Rev. Ecol. Syst. 4: 53—74.

Pianka, E. R. 1974: Evolutionary ecology. — New York.

Pianka, E. R. 1976: Competition and niche theory. — *In* R. M. May (ed.), Theoretical ecology: Principles and applications, pp. 114—141. Oxford.

Rathcke, B. J. 1976: Competition and coexistence within a guild of herbivorous insects. — Ecology 57:76—87.

Root, R. B. 1967: The niche exploitation pattern of the blue-gray gnatcatcher. — Ecol. Monogr. 37:317—350.

Schoener, T. W. 1968: The Anolis lizards of Bimini: Resource partitioning in a complex fauna. — Ecology 49:704—726.

Schoener, T. W. 1974: Resource partitioning in ecological communities. — Science 185: 27—39.

Schoener T. W. & A. Schoener 1971: Structural habitats of West Indian Anolis lizards I. Lowland Jamaica. — Breviora 368: 1—51.

Schroder, G. D. & M. L. Rosenzweig 1975: Perturbation analysis of competition and overlap in habitat utilization between Dipodomys ordii and Dipodomys merriami. — Oecologia 19:9—28.

Seifert, R. P. & F. H. Seifert 1976: A community matrix analysis of Heliconia insect communities. — Amer. Natur. 110:461—483.

Ulfstrand, S. 1976: Feeding niches of some passerine birds in a South Swedish coniferous plantation in winter and summer. — Ornis Scand. 7:21—27.

Whittaker, R. H. & S. A. Levin 1975: Editors' comments on papers 19 through 30. — *In* R. H. Whittaker & S. A. Levin (ed.), Niche: theory and application. Stroudsburg, Pa.

Wiens, J. A. 1976: Population responses to patchy environments. — Ann. Rev. Ecol. Syst. 7:81—120.

Received July 1977, revised October 1977