Species assembly in the dabbling duck (Anas spp.) guild in Finland

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Pöysä, H. 1984: Species assembly in the dabbling duck (Anas spp.) guild in Finland. — Ann. Zool. Fennici 21: 451–464.

Species composition of local dabbling duck (*Anas* spp.) assemblages in Finland were mainly composed of one, two or three species (out of six possible), and were dominated by different combinations of mallard (*A. platyrhynchos*), teal (*A. crecca*) and wigeon (*A. penelope*). Dabbling duck assemblages in more productive lakes were more closely packed in niche space than in less productive lakes. When analysed in terms of nearest-neighbour distances among all the six species in the niche space (bill morphology and neck length together) the two, three, four and five-species assemblages did not imply any competitively determined species composition. Patterns with regard to neck length were considered separately among mallard, teal, garganey (*A. querquedula*) and pintail (*A. acuta*) (species very similar in bill morphology), and among these species the competition-based prediction was supported in two-species assemblages but not very well in three-species assemblages. Very little support was found for the competitive assumption that two species would have more exclusive distributions than expected by chance from the point of view of co-occupation of a given lake by the species. Morphologically distinct species were neither particularly common regionally nor locally abundant. Results tentatively suggest that competitively structured species composition in local dabbling duck assemblages may exist among mallard, teal, garganey and pintail, but more information on niche relations among these species as well as examination of alternative biological reasons are necessary.

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1. Introduction

Local species assemblages or communities are often only small subsets of the total species pool available over a wide geographical area. They may or may not show defined structure and organization. If a non-random pattern can be recognized, a critical question arises: which factors are responsible for the pattern observed? One of the explanations most often invoked has been interspecific competition limiting the numbers and abundance of coexisting species (e.g. MacArthur 1972, Cody 1974, Schoener 1974, Diamond 1975, Gilpin & Diamond 1982, Grant & Grant 1982). It has been suggested that competition between the species in evolutionary time has led to ecological and morphological differences that contribute to the allocation of limiting resources and to stable coexistence of the species (e.g. Hutchinson 1959, Brown & Wilson 1965, Schoener 1965; but for a critical view concerning possibility of coevolution between competitors see Connell 1980). In other words, saturated communities and species arrays would be assembled through certain combination rules that strive to minimize interspecific competition (e.g. Diamond 1975; restated by Gilpin & Diamond 1982, Herrera 1981).

The competitive explanation of assembly patterns has recently been strongly criticised (e.g. Connor & Simberloff 1979, Strong et al. 1979, Simberloff & Boecklen 1981, Simberloff 1982, Wiens 1982). Critics have emphasized that explanations based on interspecific interactions have been accepted without adequately examining alternative explanations, including a critical comparison of the observed patterns with those produced randomly (i.e., without interactive effects).

Niche relations as well as relationships between ecological and morphological niche organization among six dabbling duck (*Anas* spp.) species have been studied elsewhere (Pöy-

sä 1983a, b). It appeared that bill morphology and neck length are potentially critical morphological characters in resource partitioning among the dabbling ducks. It also became evident that among the six species there are both ecologically and morphologically very similar species pairs. Furthermore, in the beginning of the breeding season, i.e. during the egg formation and laying period, the energy and nutritional requirements of breeding dabbling duck females are especially high (e.g. Krapu 1979, Owen & Reinecke 1979, Swanson et al. 1979), and an increase in the consumption of protein-rich animal food by females during this period has been documented (e.g. Krapu 1974). It is important, therefore, that adequate protein-rich food resources are available at shallow water depths when energy demands are high but the supplies of aquatic invertebrates in general are scarce (see also Swanson et al. 1979). It is thus possible that competition for food and/or suitable feeding places may be important in structuring the species composition of local breeding dabbling duck assemblages in ecological time. These findings will be used as a starting-point in the analysis of assembly patterns of the dabbling duck guild described in this paper. Several *a priori* predictions of assembly patterns formulated on the basis of competition theory are tested, in many cases against random "null" models.

2. Material and methods

2.1 Measures of ecological similarity and niche packing

Neck length and bill morphology reflect much of the feeding behaviour and food of the dabbling duck species (see Pöysä 1983a, b) and are thus good indicators of ecological similarity and niche packing among the species. In this paper I have used the same nine ratio variables of bill morphology (8 variables) and neck length (1 variable) that were used in Pöysä (1983b; table 1). Relations between the species in the morphological niche space defined by the nine ratio variables were quantified by calculating the Euclidean distances (*ED*) between all the species pairs:

$$ED_{i,j} = [\sum_{k=1}^{n} (X_{i,k} - X_{j,k})^2]^{1/2}$$

where $ED_{i,j}$ is the Euclidean distance between species i and j, $X_{i,k}$ and $X_{j,k}$ are the standardized ($\bar{x} = 0$, $\sigma^2 = 1$) values of the morphological ratio variable k for species i and j. The distance matrix is presented in Table 1 (above diagonal) and a dendrogram based on this matrix (UPGMA-method, Sneath & Sokal 1973) and showing the distance relations among the species is given in Fig. 1. Nearest-neighbour

Table 1. Euclidean distances (above diagonal) between six dabbling duck species based on nine morphological ratio variables as well as neck length ratios (beneath diagonal) for four dabbling duck species. Neck length ratios are given only for species that have structurally very similar bills.

	Ma	Te	Ga	Wi	Pi	Sh
Mallard (Ma)	–	0.268	0.219	0.406	0.201	0.603
Teal (Te)	1.675	–	0.218	0.490	0.274	0.500
Garganey (Ga)	1.596	1.049	–	0.390	0.357	0.614
Wigeon (Wi)				–	0.501	0.912
Pintail (Pi)	1.025	1.716	1.635		–	0.529
Shoveler (Sh)						–

distance (NND; two species are allowed to be each other's neighbours) was used to indicate the similarity of two species and the niche packing of a given species assemblage. In addition to the NND the ratios of neck length (NLR) between adjacent guild members (larger to smaller) were also used in comparisons made with only four species as an indicator of similarity in resource use and packing in the niche space (Table I, beneath diagonal). This was done only for the mallard *Anas platyrhynchos*, teal *Anas crecca*, garganey *Anas querquedula* and pintail *Anas acuta*, species that have structurally similar bills (see Fig. 1 and Pöysä 1983b, figs. 4 and 6).

2.2. Data base for species assemblages

Number, identity and abundance of species in local dabbling duck assemblages were derived from a number of published and some unpublished data sets (see Appendix). Only studies in which the information is given for a single lake or for a complex of two or three neighbouring lakes were included. If data for successive years are given, each year has been treated separately, e.g., a lake studied in three successive breeding seasons gives data for three dabbling duck assemblages. With this criterion, dependence between the data of successive years may bias the material used for recording species composition of dabbling duck assemblages (i.e. the abundance of different assemblage types, see section 2.3.). To minimize this problem I included data from only one year if a lake had identical dabbling duck species compositions in two successive years. With this criterion, there remained only 14 localities from which data were derived from two or more years (successive or not), and in these lakes abundance relations among the dabbling duck species did not correlate very strongly between two successive years (mean $r = +0.418 \pm 0.699$, $n = 19$). In the final material 168 out of 182 localities (with at least one dabbling duck pair) are presented with only one breeding season. It should be pointed out that when testing the shared lake hypothesis (see section 2.3.) a more extensive data base was used (see Appendix). The vast majority of the material is from inland lakes (85.7 % of localities); Region I includes 24 sea bays and Region V two river deltas. The area covered extends over the whole of Finland and thus represents the regional distribution of all the species in Finland. Possible regional variation in the assembly pattern was studied by grouping the data into five regions (see Appendix).
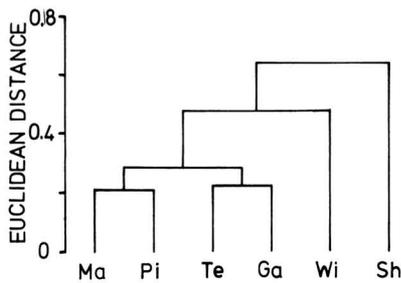
Differences in detectability between the dabbling duck

Fig. 1. A dendrogram based on nine morphological ratio variables showing the Euclidean distances between dabbling duck species. For distance matrix and species abbreviations see Table 1.

species during waterfowl censuses may cause bias in the species lists derived from census data. Effects of this problem on the results are difficult to estimate since no criteria for correcting census efficiency for different species are available. A comparison of the frequencies of occurrence of the two rare species garganey and' shoveler *Anas clypeata*, which have principally similar habitat preferences but are dissimilar with respect to detectability during censuses (in my experience the shoveler is more easily detected), suggests, however, that this bias is of minor importance in the material used here: garganey was found in 38 and shoveler in 35 out of 205 possible assemblages (see Table 2). In all the papers, except Rajala & Lindén (1978) and Haapanen & Nilsson (1979), from which data for dabbling duck assemblages were derived, the authors refer to the methodological papers by Linkola (1959) and/or Siira (1959) when describing the methods and criteria they used in waterfowl cencuses and estimation of pair numbers. Census methods used in the papers included in the present analysis have thus been at least principally similar; moreover, the methods used by Rajala & Lindén (1978) and Haapanen & Nilsson (1979) as well as by me in my unpublished counts do not differ essentially from those used in the other studies. In general, the authors have tried to make counts efficient enough to give an accurate picture of the breeding waterfowl populations in the particular lakes studied by them.

2.3. Randomization procedures

The observed NND values of local dabbling duck assemblages with different numbers of species were compared with those produced in random draws of the same number of species from the total species pool. With six species there are fifteen possible two-species, twenty possible three-species, fifteen possible four-species and six possible five-species assemblage types. In the first stage mean NND values were calculated for each possible assemblage type. Then for each assemblage size class (two, three, four and five species) the mean NND values (=expected NND values) and their standard deviations were calculated on the basis of the mean NND values of different assemblage types in each assemblage size class. The number of observed assemblages lying above or below the expected mean was also noted. The randomization procedure was principally the same when calculating the expected NLR

values for two and three-species assemblages with only four pool species.

It is worth pointing out here three potential sources of error that may bias the comparisons of observed and randomized assemblages. Firstly, because the observed and randomized assemblages were derived from the same pool of species (six or four) the two data sets are not independent. It is evident that the randomization technique used here favours the acceptance of the null hypothesis that the observed NND or NLR values do not differ from the randomized ones (see also Grant & Abbott 1980), i.e., the observed and randomized NND or NLR values are necessarily rather similar. This must be taken into account when interpreting the results. Secondly, when identifying how the individual NND and NLR values of the observed assemblages behave with respect to the expected values (i.e., greater or smaller than the expected value) medians rather than means of the expected NND and NLR values in different assemblage size classes should be used (see also Hendrickson 1981). However, with the 34 possible comparisons made in this study medians and means give similar results in 31 cases, the main conclusions thus remaining unchanged. So, for the sake of consistency, the means of the expected NND and NLR values are used throughout this paper. Thirdly, when calculating the expected values no attention was paid to the abundance relations among the species. Abundance of a given species inevitably influences the chance of the species occurring in the observed assemblages (e.g. abundance and frequency of occurrence of the species in assemblages with more than one but less than six species are positively correlated: $r = 0.914$, $P < 0.05$). Accordingly, had I included this contraint the randomization test used here would have been even more (see also the first point above) biased toward the type II error, i.e., acceptance of a false null hypothesis. To minimize this bias I gave all the species an equal, abundance-independent probability of being included in the random assemblages. For further discussion of related problems in constructing "null" models, see e.g. Grant & Abbott (1980), Hendrickson (1981), Case et al. (1983), Harvey et al. (1983) and Quinn & Dunham (1983).

A test was also performed to discover whether two species occur exclusively in lakes more often than could be expected if the species select their breeding lakes independently of each other. It is misleading to assume that all lakes and other waterfowl biotopes are equally good habitats for the dabbling duck species. Accordingly, I had to assess more realistically the value of different lakes for a particular dabbling duck species when calculating the expected number of lakes shared by two species, using all the lakes included in the present analysis. Ideally, if data of productivity and habitat structure of the lakes studied here were available, the habitat preferences of different species could be taken into account when calculating the expectations (for arguments in favour of this kind of approach in a related context see e.g. Graves & Gotelli 1983, Haila 1983, Haila & Järvinen 1983). Since such data are not available, however, I was compelled to use indirect ways to incorporate this aspect into the calculations. For the purposes of this paper I decided to use the occurrence probabilities (OP) of each dabbling duck species in lakes with different total numbers of waterfowl species, i.e., the proportion of lakes with a particular dabbling duck species was plotted for various species-richness classes (Fig. 2). Even though the connection between the total number of waterfowl species and habitat productivity/ structure may be obscure, this method seems justified as a first effort to take into account the suitability of different
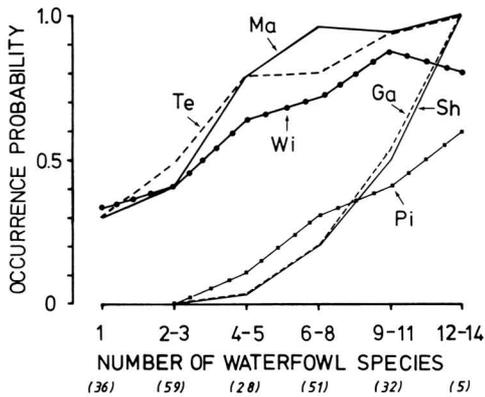
Fig. 2. Probabilities of occurrence of dabbling duck species in lakes with different numbers of breeding waterfowl species. Number of lakes in each species-richness class in brackets. For species abbreviations see Table 1.

lakes for different species. Support for this opinion can be found from the data presented by Pöyhönen (1962, tables 1 and 2). I constructed for each of the sixteen lakes studied by Pöyhönen an index of habitat structure by summing together the numbers of plus signs (which indicate the richness of a given vegetation type identified by Pöyhönen) over all the seven vegetation type columns (see Pöyhönen 1962, table 2, columns 3 to 9; for example, lake Pyhälampi has nine plus signs in all and thus has an index value of 9). The number of breeding waterfowl species in the same sixteen lakes can be found from table 1 in Pöyhönen (1962). In this small data set there is a high positive correlation between the richness of vegetation (index of habitat structure) and total number of waterfowl species: $r = 0.820$, $P < 0.001$. With regard to occurrence probabilities of dabbling ducks this is an important association since the occurrence and density of dabbling ducks are positively associated with the richness of both emergent and submerged vegetation in lakes and wetland areas (see e.g. Danell & Sjöberg 1978, Kaminski & Prince 1981, Pöysä 1983c, 1984).

The expected number of lakes shared by two species was then calculated using the equation

$$EL_{i,j} = \sum_{k}^{n} OP_{i,k} \times OP_{j,k}$$

where $EL_{i,j}$ is the expected number of lakes shared by species i and j, $OP_{i,k}$ and $OP_{j,k}$ are the probabilities of occurrence of species i and j in lake k that belongs to a certain species-richness class in Fig. 2. For example, if we have a hypothetical sample of four lakes with 5, 7, 7 and 13 waterfowls species, respectively, the expected number of lakes shared by teal and garganey is:

$EL =$
$(0.79 \times 0.04) + (0.80 \times 0.20) + (0.80 \times 0.20) + (1.0 \times 1.0) =$
1.4

This procedure in principle corresponds to that used by Gilpin & Diamond (1982). Northern regions (IV and V, see Appendix) are problematic in this respect, since the

garganey and shoveler, for example, are very rare species there and may thus simply for this reason be lacking from unproductive lakes. However, since the number of waterfowl species per lake is small in the northern regions ($\bar{x} = 3.5 \pm 1.8$ species per lake, $n = 57$) and the probabilities of occurrence of garganey and shoveler are very low in such lakes ($OP = 0.04$ for both species in lakes with 4-5 waterfowl species, see Fig. 2) the method used here when calculating the expected number of shared lakes does not give greatly overestimated expected values in those cases where these two species are included.

3. Results

3.1. Assemblage types — regional variation and patterns in different lake types

With six species there are 63 possible assemblage types (from one to six species), of which only 29 different ones were found in the whole data set (Table 2). Assemblages of one species were most frequent (34.1 %) followed by two and three-species assemblages (22.4 and 20.5 %, respectively), the four, five and six-species assemblages together forming only 23.0 % of all the 205 assemblages analysed here. The only single-species assemblages were those of either mallard, teal or wigeon *Anas penelope*. These three species were also the most frequently occurring in the assemblages of more than one but less than six species; the frequencies of occurrence as calculated from Table 2 are: mallard 88.3 %, teal 82.5 %, wigeon 73.3 %, garganey 19.2 %, pintail 17.5 % and shoveler 16.7 %.

Regional variation

I have divided the whole material into five geographically different regions. In the southernmost regions I, II and III (SW, SE and central Finland, respectively) assemblages with any number of species were found, whereas in the northern regions assemblages with more than four species are very rare (Table 2). This could also be expected on the basis of the geographical distribution of the garganey and shoveler. In region V one of the communities comprised all six species, even though garganey and shoveler are not generally found as far north (see also Haapanen & Nilsson 1979). In SW Finland assemblages of two to five species were most usual (together 89.2 %), in SE Finland assemblages of one to three species (86.5 %), in central Finland assemblages of one, three and six species (73.3 %), in southernmost Lapland (IV)

Table 2. Dabbling duck assemblage types and their frequencies in 182 waterfowl localities in different regions of Finland. Region I is SW Finland, Region II SE Finland, Region III central Finland, Region IV southern Lapland and Region V northern Lapland. For data source see Appendix and for interpretation of assemblages see Sect. 2.2. in the text. Species abbreviations are: Ma = mallard, Te = teal, Ga = garganey, Wi = wigeon, Pi = pintail, Sh = shoveler.

Assemblage type	Total area	Regions I	II	III	IV	V
1-species:						
Ma	24	2	13	6	3	
Te	22		11	3	4	4
Wi	24		13		3	8
2-species:						
Ma-Te	19	9	8	2		
Ma-Ga	1		1			
Ma-Wi	10	1	8		1	
Ma-Pi	1	1				
Ma-Sh	2	1			1	
Te-Wi	12		7		3	2
Te-Pi	1				1	
3-species:						
Ma-Te-Ga	2				2	
Ma-Te-Wi	31	4	15	6	5	1
Ma-Te-Pi	1				1	
Ma-Te-Sh	1	1				
Ma-Ga-Sh	1		1			
Ma-Wi-Pi	2				2	
Ma-Wi-Sh	3	3				
Te-Wi-Pi	1				1	
4-species:						
Ma-Te-Ga-Wi	5	2	3			
Ma-Te-Ga-Pi	1			1		
Ma-Te-Ga-Sh	2	2				
Ma-Te-Wi-Pi	10	1	1	3	2	3
Ma-Te-Wi-Sh	2	1	1			
Ma-Ga-Wi-Pi	1				1	
5-species:						
Ma-Te-Ga-Wi-Pi	2			2		
Ma-Te-Ga-Wi-Sh	8	6	2			
Ma-Te-Wi-Pi-Sh	1	1				
6-species	15	2	5	7		1
Total number of assemblages	205	37	89	30	30	19

Table 3. Dabblind duck assemblage types and their frequencies in four different lake types studied by Löfgren (1967 and unpubl.) in SE Finland. The lake types are: 1) eutrophic, 2) dystro-mixotrophic, 3) sterile dystrophic, and 4) dystrophic with sedge on the shore. For species abbreviations see legend to Table 2.

Assemblage type	Lake types 1	2	3	4
1-species:				
Ma		2	5	2
Te		4	2	3
Wi		2	2	6
2-species:				
Ma-Te		2	2	1
Ma-Ga		1		
Ma-Wi			2	2
Te-Wi			2	4
3-species:				
Ma-Te-Wi		6	2	3
Ma-Ga-Sh	1			
4-species:				
Ma-Te-Ga-Wi	2	1		
Ma-Te-Wi-Pi		1		
Ma-Te-Wi-Sh	1			
5-species:				
Ma-Te-Ga-Wi-Sh		1		
6-species	2			
Total number of assemblages	6	20	17	21

assemblages of one and three species (70.0 %) and in northernmost Lapland (V) assemblages of one species (63.1 %). Mallard, teal and wigeon were the most frequent species in all regions (Table 2).

Patterns in different lake types

Löfgren (1967 and unpubl.) provides data for dabbling duck assemblages in four different lake types from a restricted area in Region II. The lake types studied by him were: 1) clearly eutrophic; 2) dystro-mixotrophic (usually at least 1/3 of the total shore length surrounded by cultivated fields); 3) sterile dystrophic (shores usually stony or dry pine forest); and 4) dystrophic (with sedge on the shore). Dabbling duck assemblages on these four lake types are presented in Table 3. In clearly eutrophic lakes the guild was composed of three, four or six species. In dystro-mixotrophic lakes single-species assemblages of mallard, teal or wigeon were the most frequent (40 %), these three species also forming the three-species combinations (30 %). All six species occurred together in none of the dystro-mixotrophic lakes and none of the sterile dystrophic and dystrophic lakes. Assemblages with more than three species were not found in the latter two lake types. Furthermore, in these lake types, single-species assemblages of mallard, teal or wigeon were most frequent (52–53 %), these three being the only species observed in assemblages of two and three species.

Of the four lake types considered, eutrophic and dystro-mixotrophic lakes can be regarded as more productive than the sterile dystrophic

and dystrophic lakes. To study how habitat productivity affects species packing we can compare the mean NND values between these two lake type groups. It turns out that dabbling duck assemblages in the productive lakes are more closely packed than in the less productive lakes: in the pooled data of lake types 1) + 2) and 3) + 4) (see above) the mean NND values and their standard deviations are 0.294 ± 0.035 and 0.385 ± 0.089, respectively, the difference being statistically significant ($t =$ 4.08, $df = 34$, $P <0.001$). There is, however, one hidden pitfall that hinders straightforward acceptance of this result. Because the number of coexisting species is greater in the productive lakes (2–6 species) than in the less productive lakes (2–3 species), and a negative correlation is to be expected between mean NND and number of coexisting species (see e.g. Fig. 3A), the result may be obtained automatically without any connection to competitive interactions. To check this possible bias I calculated new, expected NND values for these two lake type groups, also taking into account differences in their species numbers, i.e., the expectedd mean NND value for each lake type group was calculated by weighting the mean NND of different assemblage size classes (= number of coexisting species, see section 2.3.) with their proportions from all the assemblages (with ≥ 2 species) in each lake type group. The expected mean NND value is 0.341 ± 0.097 for the productive lakes and 0.406 ± 0.160 for the less productive lakes. With these expected NND values the difference in species packing between less productive and productive lakes is $0.406-0.341 = 0.065$, the corresponding difference with the observed NND values being $0.385-0.294 = 0.091$; the difference in packing with the observed values is 40 % greater than with the expected values. This is not intended to be a rigorous test, but it suggests that the observed difference in species packing between productive and less productive lakes is greater than could be expected when differences in species numbers between these two lake type groups are also taken into account. It is interesting to note that if differences in abundances between the dabbling duck species are also taken into account (i.e., members of two, three, four and five-species assemblages are selected randomly from a species pool where the species are presented in the same proportions as they are in the total data presented by Löfgren 1967, table 1), the difference in species packing between the two

lake type groups is even clearer (the percentage difference calculated as above is then 160 %).

3.2. Niche packing — observed vs. randomized assemblages

At this stage my hypothesis is as follows. If competition is effective in structuring the species composition of dabbling duck assemblages the observed mean NND values (indicating niche packing; the greater the value the looser the packing) in two, three, four and five-species combinations should be greater than the expected ones produced through randomly selecting an equal number of species from the total species pool. This prediction is not supported when using the whole data set (Fig. 3A). The prediction can also be tested for each region separately. In sum, no support for competitively structured assemblages can be found in 13 out of 18 possible comparisons (Fig. 3B–F). So, there remain only five cases where the observed mean NND is greater than the expected one. None of these are, however, significantly greater (t-test, $P >0.20$ or greater in all cases).

We may also study how the individual observed assemblages behave with respect to the expected mean NND values; to be in favour of the competition hypothesis, a greater number of actual assemblages should lie above than below the expected mean NND values. With the whole data set only five-species assemblages support the competition hypothesis, but not significantly (Fig. 3A; two-tailed binomial test, $P = 0.066$). With regional data sets only five-species assemblages in Region I (Fig. 3B) have a distribution significantly ($P = 0.016$) consistent with the competition hypothesis (note its contribution to the result obtained with the whole data).

3.3. Co-occurrence of species — observed vs. expected number of shared lakes

We may also study coexistence of the dabbling duck species within the insular system composed of all the waterfowl localities included in the present analysis. If potential competitors interact so strongly that they are not able to co-occupy a given lake we may predict that the observed number of lakes shared by two species is smaller than the expected number of lakes shared when the species occupy a given lake independently
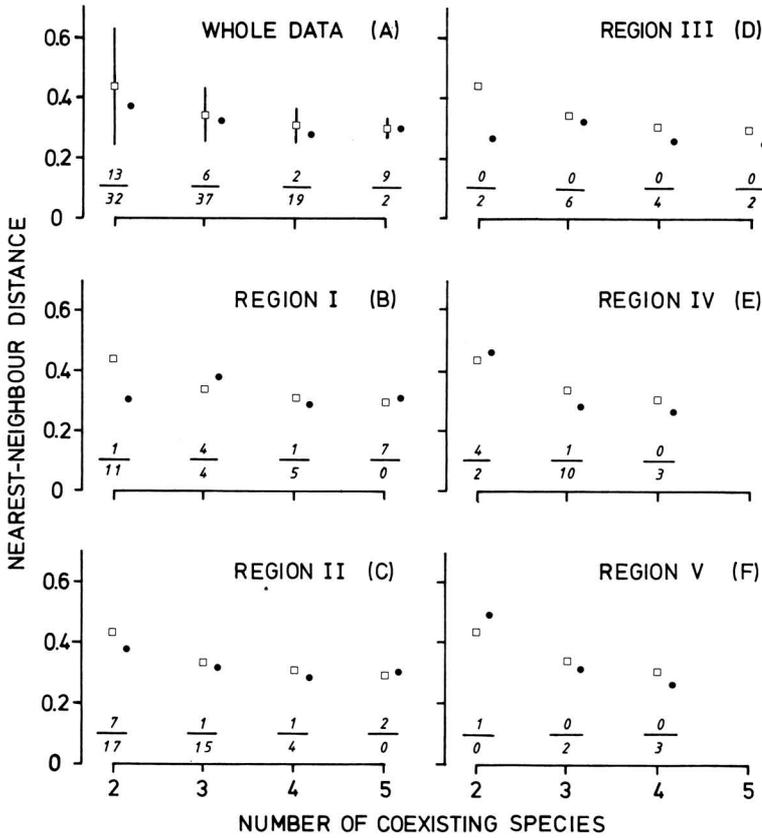
Fig. 3. Observed (black dots) and expected (open squares) mean nearest-neighbour distances (NND) for dabbling duck assemblages with different numbers of coexisting species in the whole data set (A) and in different regions (B-F). Standard deviations of expected NND values are also indicated in (A). Regions are the same as in Table 2. All observed NND values either greater (above) or smaller (below) than the mean expected NND value are presented at the bottom of each section of the figure. For calculation of the expected NND values see Sect. 2.3.

from each other (see section 2.3.). Both the actual and expected values are presented for all species pairs in Table 4. We can see that in only two cases, viz., mallard vs. teal and teal vs. wigeon, is the observed number of lakes shared smaller, but not significantly (χ^2 test) smaller than the expected one. In all the other cases the opposite is true, in two cases, viz., garganey vs. pintail and garganey vs. shoveler even significanly so ($\chi^2 = 4.87$, $P < 0.05$ and $\chi^2 = 9.06$, $P < 0.001$, respectively). Altogether, the number of actual values smaller than the predicted values is significantly greater than could be expected on the basis of the 1:1 distribution ($\chi^2 = 8.07$, $P < 0.01$).

Table 4. Observed (first entry) and expected (second entry) number of shared lakes for dabbling duck species among all the waterfowl localities included in the present analysis. For calculation of the expected number of lakes shared by two species see Sect. 2.3., and for species abbreviations see legend to Table 2.

	Ma	Te	Ga	Wi	Pi
Te	112/114.1	–			
Ga	41/33.0	38/31.4	–		
Wi	101/100.6	96/97.1	34/27.9	–	
Pi	38/34.5	36/30.7	22/13.8	36/28.3	–
Sh	38/31.9	32/30.4	29/16.7	32/27.1	19/13.5

3.4. Patterns among the four species critical in terms of bill morphology

We have so far analysed the assembly patterns among all the six dabbling duck species using the NND calculated on the basis of nine morphological ratio variables as an indicator of niche packing in local dabbling duck assemblages. Wigeon and shoveler differ drastically in bill morphology from the other species as well as from each other. In contrast the four remaining species, viz., mallard, teal, garganey and pintail, have structurally rather similar bills (see e.g. Pöysä 1983b), and are thus more obviously potential food competitors. Taking this into account, in this section I consider the coexistence of these four species in relation to differences in neck length, which is a potentially critical morphological character in vertical partitioning of the feeding habitat (see Pöysä 1983a, b). The shared lake hypothesis will also be considered a little closer among these four species.

When testing the competitive explanation I follow the strategy adopted above and hypothesize first that, if competition is strong enough among these four species (with regard to their similar bill morphologies), it should be revealed in the pattern of ratios of neck length so that the mean NLR between adjacent members is greater in the actual assemblages than in the randomly constructed ones. In two-species assemblages the observed NLR values are greater in the pooled data set as well as in all the regions where they were found than in the random two-species assemblages, although the difference is statistically significant only in Region II (Table 5). In three-species assemblages the observed NLR values are very close to the random expectations.

The number of actual two and three-species assemblages lying above or below the expected mean NLR can also be found from Table 5. In two-species assemblages the distribution is significantly (two-tailed binomial test, $P < 0.008$) directed in agreement with the competition hypothesis in the whole data set and in Regions I, II and III. In all the other comparisons the distribution is either non-significant or in contrast with the competition hypothesis.

It became apparent from Table 4 that in the whole data set pooled over all the Regions I–V, mallard and teal actually shared a slightly smaller number of lakes than expected. Table

Table 5. Observed mean neck length ratios (NLR) for two and three-species combinations comprising mallard, teal, garganey and pintail in dabbling duck assemblages in different regions in Finland. N gives the number of NLR values that were either greater (first entry) or smaller (second entry) than the expected mean. The regions are the same as in Table 2. t-test results of comparisons between observed and expected mean NLR values are also indicated. For calculation of the expected values see Sect. 2.3.

	N	Mean	SD	t
2-species				
Whole data	57/3	1.641	0.143	2.035 *
Region I	15/1	1.634	0.163	1.318 ns
Region II	26/0	1.669	0.021	2.844 **
Region III	8/0	1.675	0.000	1.574 ns
Region IV	7/2	1.540	0.292	0.265 ns
Region V	1/0	1.675	0.000	0.508 ns
Expected		1.499	0.321	
3-species				
Whole data	12/18	1.333	0.014	0.134 ns
Region I	2/10	1.328	0.011	0.533 ns
Region II	1/5	1.328	0.011	0.443 ns
Region III	3/0	1.350	0.000	1.683 ns
Region IV	3/3	1.335	0.018	0.273 ns
Region V	3/0	1.350	0.000	1.683 ns
Expected		1.332	0.018	

6 depicts by region both the actual and expected number of lakes shared by two species. It appears that in Region I the species will co-occupy a given lake less frequently than expected; difference is significant, however, only for mallard vs. pintail ($\chi^2 = 5.01$, $P < 0.05$) and for teal vs. pintail ($\chi^2 = 5.60$, $P < 0.025$). The same is also true for mallard vs. teal in Regions IV and V and for garganey vs. mallard, teal and pintail in Region V, but in none of these cases is the difference between the actual and expected numbers significant.

3.5. Local abundance, regional commonness and morphological uniqueness

We may first test whether the species that are most abundant are also most clearly morphologically segregated from the other species, i.e., if species abundances are positively correlated with the mean Euclidean distance calculated for each species in relation to the rest of the species. This is not supported by the data (Fig. 4).

This topic can be considered more closely in the recent theoretical framework by Hanski (1982a). Hanski has presented a hypothesis according to which species in communities

Table 6. Observed (first entry) and expected (second entry) number of shared lakes for four dabbling duck species in different regions in Finland. The regions are the same as in Table 2. For calculation of the expected number of lakes shared by two species see Sect. 2.3., and for species abbreviations see Table 2.

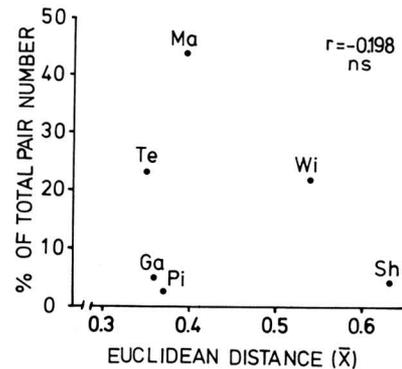| Region		Ma	Te	Ga
I	Te	29/30.8		
	Ga	12/14.3	12/13.7	
	Pi	5/13.1	4/12.3	2/6.3
II	Te	38/31.6		
	Ga	15/6.5	13/6.2	
	Pi	9/7.0	9/5.3	8/3.0
III	Te	27/23.9		
	Ga	10/7.3	10/6.9	
	Pi	13/8.0	13/7.3	10/2.8
IV	Te	12/18.9		
	Ga	3/2.2	2/1.9	
	Pi	7/3.9	6/3.4	1/0.6
V	Te	6/8.9		
	Ga	1/2.8	1/2.8	
	Pi	4/2.5	4/2.4	1/1.1

Fig. 4. Relationship between relative abundance and morphological uniqueness among dabbling duck species. Abundance relations are calculated from the total pair numbers of dabbling ducks in the waterfowl communities included in the present study; morphological uniqueness of each species is calculated as the mean Euclidean distance from the rest of the species. For calculation of Euclidean distances see Sect. 2.1. in the text and for species abbreviations Table 1.

Table 7. Local abundance (LA), regional commonness (RC) and the "core" (c) and "satellite" (s) species status of six dabbling duck species in three regions in Finland. The regions are the same as in Table 2; data for Region I ($n = 37$) is from Suoranta & Rautanen (1980), for Region II ($n = 26$) from Löfgren (1967 and unpubl., only eutrophic and dystro-mixotrophic lakes), for Region IV ($n = 15$) from Rajala & Lindén (1978 and unpubl.). Local abundance is indicated by the mean density (pairs/km²) of the species and regional commonness by the frequency of occurrence of the species in waterfowl communities of the regions. The correlation coefficients between local abundance and regional commonness are also presented for each region at the bottom of the table. For further details see text.

	Region I		Region II		Region IV	
	LA	RC	LA	RC	LA	RC
Mallard	32.2	100.0 c	6.5	76.9 c	0.24	60.0 c
Teal	7.6	78.4 c	6.3	76.9 c	0.67	80.0 c
Garganey	1.4	32.4 s	4.8	26.9 s	0.01	6.7 s
Wigeon	3.9	56.8 c	6.1	65.4 c	0.34	66.7 c
Pintail	0.2	13.5 s	2.1	11.5 s	0.10	46.7 s
Shoveler	2.7	48.6 s	1.4	19.2 s	0.01	6.7 s
LA vs. RC	$r = 0.836$		$r = 0.910$		$r = 0.878$	
	$P < 0.05$		$P < 0.05$		$P < 0.05$	

can, on the basis of their local abundance and regional distribution, be grouped into two distinct types: the "core" species, which are regionally common and locally abundant, and

are also relatively well spaced out in niche space; and the "satellite" species, which are characterized by contrasting attributes. We may predict that if competition is important in structuring the dabbling duck guild, core species should be better spaced out in niche space than the equal number of species randomly drawn from the total species pool.

The hypothesis was tested with data from Regions I, II and IV. To make the assumption of equal habitat selection of the species more accurate (see Hanski 1982a, b), I have excluded from the Region II data the Löfgren (1967) lake types 3) and 4) (see section 3.1.). Local abundance and regional distribution of the species are significantly correlated in all the three regions, and the same three core species can be identified for all regions, viz., mallard, teal and wigeon (Table 7, see also section 3.1.). Accordingly, we need only one test and the result is that the three core species just mentioned are not better spaced out in niche space than those selected at random from the species pool: the mean NND values and their standard deviations for the actual and random core species are 0.314 and 0.338±0.093, respectively. Actually, the three satellite species (see Table 7) are better (although not significantly) spaced out in niche space (mean NND = 0.414) than both the randomly selected and the observed three core species.

4. Discussion

The analysis of assembly patterns among six dabbling duck species revealed some determined structure in both the number and identity of species in local dabbling duck assemblages. One general feature of local assemblages seemed to be that they were mainly composed of one, two or three species, which were dominated by different combinations of mallard, teal and wigeon. The decrease in the number of coexisting species towards both more northern regions and less productive lake types also appeared to be generally true.

The following is a deeper discussion of four predictions concerning the possible manifestations of interspecific competition in structuring the dabbling duck guild.

1) In the light of competition theory more productive environments offer more resources to be shared, allowing greater dietary specialization, and will thus harbor more species and lead to closer niche packing (MacArthur 1970, 1972).

The dabbling duck assemblages of more productive lakes were more closely packed in niche space than assemblages of less productive lakes. Accordingly, there seems to be support for the assumption that resource richness contributes to the coexistence of potential competitors (i.e. morphologically closely related species). In sterile lakes, suitable feeding places together with shortage of food supplies might be the limiting resources to be competed for. Only mallard, teal and wigeon were found to occupy less productive lakes. It is interesting to note that in two cases the species that drops out of the guild in the sterile lakes is one from the morphologically most similar species pairs, viz. pintail from the mallard and pintail, and garganey from the teal and garganey. Of the six dabbling duck species, the wigeon feeds most selectively on plant material and the shoveler on animal material, whereas proportions of plant and animal food eaten by mallard, teal, garganey and pintail vary much more (see references cited in Cramp & Simmons 1977). In terms of bill morphology, the wigeon and shoveler differ clearly from each other as well as from the remaining four species. These four have structurally rather similar bills, which are probably adapted to omnivorous food habits (see Pöysä 1983b). It seems reasonable to assume that the wigeon and shoveler are not disposed to intense food competition, but

among the remaining four species competition for food may play a role under some conditions. The generalistic relations among the species in feeding ecology (feeding habitat and method) are: wigeon > mallard > teal > pintail > shoveler > garganey (Pöysä unpubl.). As a herbivorous, generalized and semi-terrestrial species the wigeon is at an advantage in many lake types, also in less productive ones. The absence of the shoveler from the sterile lakes may be due to the fact that, because of its large body size, and as a specialist in feeding habitats and methods as well as in food choice (see Pöysä 1983a, b), it cannot find sufficient food in the less productive lake types. Among mallard, teal, garganey and pintail competition for suitable feeding habitats and/or food may be too strong in sterile lakes, and the ecologically more generalized species (mallard and teal) would under these circumstances dominate over the specialized species (garganey and pintail).

The situation is not, however, that simple. In comparisons between productive and less productive lake types it was assumed that the occurrence of all six dabbling duck species in any of the lake types was independent of any possible autecological constraints on the species. For example, the occurrence of garganey, pintail and shoveler in sterile lakes is an extremely rare phenomenon in southern Finland even if the lake contains no potential competitor; even in the little data used here there were six empty sterile lakes (Löfgren unpubl.). It is thus not out of the question that some autecological constraint on garganey, pintail and shoveler may keep these species away from the more sterile lakes.

Two further points concerning breeding habitat selection of the pintail and garganey in regions with different densities and abundances of mallard and teal are worth mentioning here. Firstly, in a comparison of Region IV and the area studied by Löfgren (1967) the overall densities of mallard and pintail are: c. 0.2 pairs/km² and c. 5.0 p./km² for mallard, and c. 0.1 p./km² and 0.2 p./km² for pintail, respectively. Now, it seems that in Region IV, where the density of mallard is about 25 times smaller, the pintail also occurs (although rarely) in less productive lake types even though its overall density is even smaller there (checked from the unpublished material by Rajala & Lindén). Secondly, in the Łęczna-Włodawa Lake District in Poland the garganey may also be found as a breeding species in lakes with

dystrophic or oligotrophic properties where the teal is not found (Dyrcz et al. 1973, p. 343). These are, of course, only single observations, but interesting in this context. They suggest that in some regions interspecific relations may be of concern in the habitat distribution of garganey and pintail. They are not, however, evidence of competitive displacement, since factors other than competition have not been considered. More accurate data on habitat selection of these species in different parts of their regional distribution are needed before drawing any conclusions on explanatory reasons.

2) Spacing of species in the morphologically defined niche space should be looser in the actual assemblages than in the randomly constructed assemblages of equal size.

As stated earlier (see section 2.3), the randomization technique used here is perhaps not the most powerful one when one wants to distinguish patterns produced competitively from random ones. Principally similar techniques with different applications and constraints have been used in many recent papers dealing with the testing of competitive interactions in animal communities (e.g. Strong et al. 1979, Ricklefs & Travis 1980, Bowers & Brown 1982, Hanski 1982b, c, Ranta 1982a, b, Ranta & Tiainen 1982, Case et al. 1983). In the present study the vast majority of the observed mean NND values (indicating the closeness of species packing in niche space) were, like those of the individual NND values, smaller than the expected random ones, i.e., opposite to the prediction formulated on the basis of competition theory. This suggests that the two, three, four and five-species assemblages do not imply any competitively determined species composition when analysed in terms of the nearest-neighbour distances among all the six dabbling duck species in the morphologically defined niche space. Considering the assumptions mentioned above about the liability of different species to compete for food with other species, this interpretation may, however, be only partially acceptable. The inclusion of the wigeon and shoveler in the analysis may confuse possible competitively constructed associations among the remaining four species.

Patterns in neck length were considered separately among the mallard, teal, garganey and pintail, all of which possess very similar bill morphologies and are thus potential competitors for food. Among these four species the competition-based prediction was supported in two-species assemblages but not in three-species assemblages. Two-species assemblages were found in lakes with a smaller number of breeding waterfowl species than in lakes where three or all four species occurred together (Pöysä unpubl.). If the total number of breeding waterfowl species can be used as an indicator of the trophic status of a given lake, which seems warranted (see Löfgren 1967, Nilsson & Nilsson 1976, 1978), the difference between the patterns of two and three-species assemblages agrees with the assumption that in less productive lakes resources may be in too short supply to support two morphologically very closely related species.

3) The observed number of lakes shared by two species should be smaller than the expected number of lakes shared by chance.

Distributional patterns of animal species on islands have been frequently used to find competitive interactions between species (e.g. Diamond 1975, Simberloff 1978, Connor & Simberloff 1979, Alatalo 1982, Diamond & Gilpin 1982, Gilpin & Diamond 1982, Schluter & Grant 1982, Wright & Biehl 1982). This approach has been applied here to study the co-occurrence of dabbling duck species in lakes, i.e. on patchily distributed habitat islands to which the theory of island biogeography seems applicable (for examples see Haila et al. 1982). The result was clear when all six dabbling duck species were considered together with the pooled data: there was no support for the prediction, rather the opposite. Again, the shared lake hypothesis was tested region by region separately with the four most potential competitors. Among these species the prediction was partially supported in Region I but not in the other regions. It can be seen in Table 2 that, in all, the occurrence of a rare species (garganey or pintail) in a lake lacking an abundant species (mallard or teal) is an extremely rare phenomenon. The negative signs for the observed minus the expected numbers of lakes shared as well as the general agreement between the values may thus largely be a consequence of the criterion by which the probabilities of occurrence were calculated for each species in a particular lake while calculating the expected number of shared lakes. In other words, the probabilities of occurrence of the rare species (garganey and pintail) may be influenced by competitive exclusion directed from the abundant species (mallard and teal), i.e., the common and abundant species will restrict the overall commonness and abun-

dance of the rare species.

In a consideration of the co-occupation of a given lake by the dabbling duck species, rather little support was found for the competitive assumption that the species would have more exclusive distributions than to be expected by chance alone. However, although the garganey and pintail were only occasionally found to occupy a lake without the most probable competitor being present (teal and mallard, respectively), an unsolved problem remains if competitive exclusion accounts for the fact that these species shared only lakes rich in food (see also section 1) above).

4) According to Hanski's (1982a) core-satellite species hypothesis "core" species (regionally common and locally abundant compared to the "satellite" species) in animal communities should be better spaced-out in the niche space than an equal number of species randomly drawn from the total species pool.

This hypothesis has been supported with some European and North American bumblebee communities analysed in terms of proboscis length differences (Hanski 1982b, c, but see Ranta 1982a, Ranta & Tiainen 1982) but not with animal communities in rock pools analysed in terms of differences in body size (Ranta 1982b). The results of the present study did not support the hypothesis. In contrast, if we expect more intense competition between species that are more similar morphologically, it seems that regional commonness and local abundance are not determined through competitive interactions in the dabbling duck guild. This conclusion was also supported by a direct comparison between the abundance and morphological distinctiveness of the species: morphologically distinct species did not enjoy greater abundance. Rather, it seems warranted that the consideration of abundance relations in the dabbling duck guild can be reduced to

the reciprocal patterns in two species pairs composed of morphologically very similar species, viz. mallard and pintail, and teal and garganey.

To summarize, if the six dabbling duck species are considered simultaneously there is very little support for the statement that competitive interactions between the species would structure the species composition of local dabbling duck assemblages. Furthermore, regional commonness and local abundance did not seem to be competitively determined; at least the pure presence/absence data combined with abundance relations among the six species were not sufficient to make the occurrence of competition detectable with the data treatment used in this paper. However, sufficient definite non-random assembly patterns in terms of neck length and along a habitat productivity gradient were found among the four species mallard, teal, garganey and pintail to make an outright rejection of the competition hypothesis unwarranted. An interesting question remains: why are the garganey and pintail so rare compared to the morphologically closely related species teal and mallard both regionally and locally in the regions studied? This calls for a more detailed study of the niche relations between these species in local communities. Because of the lack of data we are, of cource, also left with the problem of the extent to which the mortality in wintering and migratory areas limit the northern breeding dabbling duck populations, thus making them unlimited by resources.

References

Alatalo, R. 1982: Bird species distributions in the Gal apagos and other archipelagoes: competition or chance? — Ecology 63:881–887.

Antikainen, E. O. 1966: On abundance and dominance of waterfowl in eutrophic lakes at Riistavesi in Northern Savo. — Ornis Fennica 43:124–130. (In Finnish with English summary).

Bowers, M. A. & Brown, J. H. 1982: Body size and coexistence in desert rodents: chance or community structure? — Ecology 63:391–400.

Brown, W. L., Jr. & Wilson, E. O. 1956: Character displacement. — Syst. Zool. 5:49–64.

Case, T. J., Faaborg, J. & Sidell, R. 1983: The role of body size in the assembly of West Indian bird communities. — Evolution 37:1062–1074.

Cody, M. L. 1974: Competition and the structure of bird communities. — Princeton Univ. Press, Princeton, New Jersey.

Connell, J. H. 1980: Diversity and the coevolution of competitors, or the ghost of competition past. —

Oikos 35:131-138.

Connor, E. F. & Simberloff, D. 1979: The assembly of species communities: chance or competition? — Ecology 60:1132-1140.

Cramp, S. & Simmons, K. E. L. (eds.) 1977: The birds of the western palearctic. Vol. 1. — Claredon Press, Oxford.

Danell, K. & Sjöberg, K. 1978: Habitat selection by breeding ducks in boreal lakes in northern Sweden. — Viltrevy 10:161-190.

Diamond, J. 1975: Assembly of species communities. — In: Cody, M. L. & Diamond, J. (eds.), Ecology and evolution of communities: 342-444. Harvard Univ. Press, Cambridge, Mass.

Diamond, J. & Gilpin, M. E. 1982: Examination of the "null" model of Connor and Simberloff for species co-occurrence on islands. — Oecologia (Berl.) 52:64-74.

Dyrcz, A., Okulewicz, J. & Wiatr, B. 1973: Birds breeding in the Łęczna-Włodawa Lake District (including a quantitative study on low peats). — Acta Zool. Cracov. 18:399-474.

Gilpin, M. E. & Diamond, J. M. 1982: Factors contributing to non-randomness in species co-occurrences on islands. — Oecologia (Berl.) 52:75-84.

Grant, P. R. & Abbott, I. 1980: Interspecific competition, island biogeography and null hypotheses. — Evolution 34:332-341.

Grant, B. R. & Grant, P. R. 1982: Niche shifts and competition in Darwin's finches: Geospiza conirostris and congeners. — Evolution 36:637-657.

Graves, G. R. & Gotelli, N. J. 1983: Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. — Oikos 41:322-333.

Haapanen, A. & Nilsson, L. 1979: Breeding waterfowl populations in northern Fennoscandia. — Ornis Scand. 10:145-219.

Haila, Y. 1983: Land birds on northern islands: a sampling metaphor for insular colonization. — Oikos 41:334-351.

Haila, Y. & Järvinen, O. 1983: Land bird communities on a Finnish island: species impoverishment and abundance patterns. — Oikos 41:255-273.

Haila, Y., Hanski, I., Järvinen, O. & Ranta, E. 1982: Insular biogeography: a Northern European perspective. — Acta Oecol. (Oecol. Gen.) 3:303-318.

Hanski, I. 1982a: Dynamics of regional distribution: the core and satellite species hypothesis. — Oikos 38:210-221.

—"— 1982b: Communities of bumblebees: testing the core-satellite species hypothesis. — Ann. Zool. Fennici 19:65-73.

—"— 1982c: Structure in bumblebee communities. —Ann. Zool. Fennici 19:319-326.

Harvey, P. H., Colwell, R. K., Silvertown, J. W. & May, R. M. 1983: Null models in ecology. — Ann. Rev. Ecol. Syst. 14:189-211.

Hendrickson, J. A., Jr. 1981: Community-wide character displacement reexamined. — Evolution 35:794-810.

Herrera, C. M. 1981: Combination rules among western European Parus species. — Ornis Scand. 12:140-147.

Hutchinson, G. E. 1959: Homage to Santa Rosalia or why are there so many kinds of animals. — Amer. Nat. 93:145-159.

Kaminski, R. M. & Prince, H. H. 1981: Dabbling duck and aquatic macroinvertebrate responses to manipula-

ted wetland habitat. — J. Wildl. Managem. 44:1-15.

Kauhanen, H. 1969: Über die Wasservogelfauna an einigen eutrophischen Seen in der Gegend von Iisalmi in Nord-Savo. — Ornis Fennica 46:132-135. (In Finnish with German summary).

Kauppinen, J. 1973: Muutamien Kiuruveden järvien linnuston suhteista. — Savon Luonto 5:61-69.

—"— 1976: The bird fauna of two eutrophic lakes in central Finland. — Lintumies 11:46-50. (In Finnish with English summary).

Krapu, G. L. 1974: Feeding ecology of pintail hens during reproduction. — Auk 91:278-290.

—"— 1979: Nutrition of female dabbling ducks during reproduction. — In: Bookhout, T. A. (ed.), Waterfowl and wetlands — an integrated review: 59-70.

Lahtinen, A. 1973: Vilppulan Suojärven linnustosta. — Suomenselän Linnut 8:15-20.

Linkola, P. 1959: Zur Methodik der quantitativen Vogelforschung in den Binnengewässern. — Ornis Fennica 36:66-78.

Löfgren, S. 1967: On the composition of the bird fauna on lakes and ponds in Lappeenranta, south-eastern Finland. — Ornis Fennica 44:99-106. (In Finnish with English summary).

MacArthur, R. H. 1970: Species packing and competitive equilibrium for many species. — Theor. Pop. Biol. 1:1-11.

—"— 1972: Geographical ecology. — Harper and Row, New York.

Nilsson, S. G. & Nilsson, I. N. 1976: Hur skall naturområden värderas? Exempel från fågellivet i sydsvenska sjöar. — Fauna och Flora 71:136-144.

—"— 1978: Breeding bird community densities and species richness in lakes. — Oikos 31:214-221.

Owen, R. B. & Reinecke, K. J. 1979: Bioenergetics of breeding dabbling ducks. — In: Bookhout, T. A. (ed.), Waterfowl and wetlands — an integrated review: 71-93.

Pöyhönen, O. 1962: Die Vogelfauna in einigen Binnengewässern Mittel-Finnlands. — Ornis Fennica 34:67-77. (In Finnish with German summary).

Pöysä, H. 1983a: Resource utilization pattern and guild structure in a waterfowl community. — Oikos 40:295-307.

—"— 1983b: Morphology-mediated niche organization in a guild of dabbling ducks. — Ornis Scand. 14:317-326.

—"— 1983c: The structure of a waterfowl community in relation to habitat structure in SE Finland. — Suomen Riista 30:5-14. (In Finnish with English summary).

—"— 1984: Temporal and spatial dynamics of waterfowl populations in a wetland area — a community ecological approach. — Ornis Fennica (in press).

Quinn, J. F. & Dunham, A. E. 1983: On hypothesis testing in ecology and evolution. — Amer. Nat. 122:602-617.

Rajala, P. & Lindén, H. 1978: Riistataloudellinen selvitys Ounasjokeen suunniteltujen voimalaitosten padotus- ja allasalueilta. —Riistantutkimusosaston Tiedonantoja 6:1-33.

Ranta, E. 1982a: Species structure of North European bumblebee communities. — Oikos 38:202-209.

—"— 1982b: Animal communities in rock pools. — Ann. Zool. Fennici 19:337-347.

Ranta, E. & Tiainen, M. 1982: Structure in seven bumblebee communities in eastern Finland in relation to

resource availability. — Holarctic Ecol. 5:48–54.

Ricklefs, R. E. & Travis, J. 1980: A morphological approach to the study of avian community organization. — Auk 97:321–338.

Schluter, D. & Grant, P. R. 1982: The distribution of Geospiza difficilis in relation to G. fuliginosa in the Gal apagos islands: tests of three hypotheses. — Evolution 36:1213–1226.

Schoener, T. W. 1965: The evolution of bill size differences among sympatric congeneric species of birds. — Evolution 19:189–213.

—"— 1974: Resource partitioning in ecological communities. — Science 185:27–39.

Siira, J. 1959: Notes concerning the census of breeding populations of species of the genus Anas. — Ornis Fennica 36:98–107. (In Finnish with English summary).

Simberloff, D. S. 1978: Using island biogeographic distribution to determine if colonization is stochastic. — Amer. Nat. 112:713–726.

—"— 1982: The status of competition theory in ecology. — Ann. Zool. Fennici 19:241–253.

Simberloff, D. S. & Boecklen, W. 1981: Santa Rosalia reconsidered: size ratios and competition. — Evolution 35:1206–1228.

Sneath, P. & Sokal, R. 1973: Numerical taxonomy. — W. H. Freeman, San Francisco.

Strong, D. R., Jr., Szyska, L. A. & Simberloff, D. S. 1979: Tests of community-wide character displacement against null hypotheses. —Evolution 33:897–913.

Suoranta, A. & Rautanen, H. 1980: Lintuvesi-inventoinnit Varsinais-Suomessa vuosina 1970–77. — Turun Lintutieteellinen Yhdistys, Turku.

Swanson, G. A., Krapu, G. L. & Serie, J. 1979: Foods of laying female dabbling ducks on the breeding grounds. — In: Bookhout, T. A. (ed.), Waterfowl and wetlands — an integrated review: 47–57.

Tossavainen, T. & Tossavainen, M. 1978: Vetelin Räyringinjärven linnusto vuosina 1976–78. — Suomenselän Linnut 13:120–122.

Wiens, J. A. 1982: On size ratios and sequences in ecological communities: Are there no rules? — Ann. Zool. Fennici 19:297–308.

Wright, S. J. & Biehl, C. C. 1982: Island biogeographic distributions: testing for random, regular, and aggregated patterns of species occurrence. — Amer. Nat. 119:345–357.

Appendix. Sources of the data on dabbling duck assemblages in different regions. Note that some studies comprising more than one breeding season include lakes that have been studied every year but no breeding dabbling ducks have been recorded; such "empty years" have been omitted from the present paper. If a lake had identical dabbling duck species composition in two successive years, only one of these years was included for recording species composition of dabbling duck assemblages (see section 2.2.); however, all years (additional years in parenthesis) have been included for testing the shared lake hypothesis (see section 2.3.).

Source	Localities studied
Region I: SW Finland	
Suoranta & Rautanen 1980	13 lakes, 1 year
	24 sea bays, 1 year
Region II: SE Finland	
Löfgren 1967 and unpubl.	64 lakes, 1 year
Pöysä 1983a	1 lake, 1 year (+3)
Pöysä unpubl.	24 lakes, 1 year
Region III: central Finland	
Antikainen 1966	1 lake, 2 years
	2 lakes, 1 year (+1 for one lake)
Kauhanen 1969	3 lakes, 1 year
Kauppinen 1973	4 lakes, 1 year
Kauppinen 1976	1 lake, 1 year (+3)
Lahtinen 1973	1 lake, 4 years (+1)
Pöyhönen 1962	10 lakes, 1 year (+1 for nine lakes)
Tossavainen & Tossavainen 1978	1 lake, 2 years (+1)
Region IV: southern Lapland	
Haapanen & Nilsson 1979	2 lakes, 1 year
Rajala & Lindén 1978 and unpubl.	4 lakes, 3 years
	5 lakes, 2 years (+1 for three lakes)
	6 lakes, 1 year (+2 for one lake)
Region V: northern Lapland	
Haapanen & Nilsson 1979	1 river delta, 3 years
	1 river delta, 2 years (+1)
Pöysä unpubl.	12 lakes, 1 year (+1 for two lakes)
	1 lake, 2 years