Species composition and size of dabbling duck (*Anas* spp.) feeding groups: are foraging interactions important determinants?

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The species composition and size of dabbling duck (*Anas* spp.) feeding groups were studied to find out whether they are shaped by foraging interactions (intra- and interspecific) between group members. In some species pairs the species associations (presence/absence data) and the correlations between individual numbers suggested interspecific interaction, harmful or beneficial. When foraging niche relations (niche similarities and shifts in terms of feeding site, method and depth) between the species were used as indicators of the species most likely to interact, it became evident that interspecific foraging interactions were not consistently important in shaping the mixed species feeding groups. The comparisons suggested beneficial foraging interaction affecting coexistence and/or numerical relations in three of fifteen possible species pairs.

The feeding depth of some species was significantly greater in the largest groups. Two explanations for this difference are suggested: the use of less profitable (according to feeding depth) parts of the feeding patch was greater in very large groups, and/or the food density at or near the water surface decreased in large groups, presumably due to consumption and disturbance of the prey by the foraging ducks. These hypotheses were studied more closely in two species; both were plausible for the Teal *Anas crecca*, whereas the second was more probable for the Shoveler *Anas clypeata*. It is suggested that these factors causing an increase in feeding depth are important in limiting the size of dabbling duck feeding groups.

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Introduction

Foraging in single-species or mixed groups is common in many bird species. Feeding groups may form either via attraction of birds to foraging individuals of their own or other species, or in response to some localized concentration of food resources, without interaction between flock members (i.e. aggregations; see Morse 1970, 1977, Moriarty 1976, Caldwell 1981, Hoffman et al. 1981).

Group foraging can facilitate feeding and/or reduce the danger of predation, which makes it advantageous for an individual to join a group (for reviews see Moriarty 1976, Morse 1977, Bertram 1978, Pulliam & Millikan 1982, Pulliam & Caraco 1984). These advantages are often similar in single-species and mixed groups. However, foraging in groups may involve costs that often increase with group size and may limit the size of the group. For example, in large groups the members may make the prey less available to each other by disturbing it or by depressing its density below a critical level (e.g. Goss-Custard 1976, 1980, Hoffman et al. 1981, Waite 1984).

Foraging in large groups or at high bird densities may also compel some individuals to use less profitable parts of the feeding area (e.g. Zwarts 1976, Goss-Custard et al. 1982). In mixed-species groups, competition for food may exist between individuals belonging to different species (e.g. Morse 1970, Alerstam et al. 1974, Wiley 1980, Alatalo 1981) or there may be other forms of interspecific foraging interference (e.g. Barnard & Stephens 1981, Barnard et al. 1982). Such harmful interspecific interactions may control the species composition and size of the groups.

Feeding groups of dabbling ducks (*Anas* spp.) may be structured by interactions between group members, as shifts in foraging niches have indicated interaction between species in mixed groups (Pöysä 1985, 1986). Using results of my earlier studies on foraging niche relations among dabbling ducks (Pöysä 1983a, b, 1986) to predict the species most likely to interact, I will attempt to answer the question: Do interspecific interactions (harmful or beneficial) have any effect on the species composition and numerical relations among the species in feeding groups? In addition, I will examine some aspects of foraging behaviour that may limit the size of the feeding groups.

Material and methods

All the data are from a shallow and eutrophic wetland area (Siikalahti in SE Finland; 61°33 N, 29°33 E) described in detail elsewhere (see Pöysä 1983a, c, 1984a). In fact, the material is from the same small (c. 0.67 ha) enclosed bay that was the study area in Pöysä (1986). Being surrounded by dense *Typha latifolia* L. stands and clearly suboptimal (too deep) as a feeding habitat for dabbling ducks, this bay serves as a reasonably distinct feeding patch.

Through June, July and August in 1980, 1982 and 1983 (data from all the years pooled) I recorded the numbers of foraging individuals of each dabbling duck species present in the bay, at average intervals of 18 (SD = 13) min; at most of these recordings I also made notes of the feeding methods of each individual (picking from surface, straining from surface, bill submerged, head submerged, neck submerged, up-ending; see Fig. 1). In this paper a collection of dabbling ducks foraging in the bay at a given recording is defined as a feeding group ("groups" of 1 individual included). However, since both the species composition and the numbers of each species are evidently correlated between the successive recordings of a given recording period (lasting about 25–270 min; usually one per day), I used certain criteria before accepting data from a given recording as a "separate" feeding group: for species number, only those recordings were included that differed from the previous recording in at least one species and for group size only those that differed in the total number of individuals; if three or more successive recordings had an identical species composition and/or group size, only the data from the first recording were included. For statistical tests of association and correlation in the number of individuals between two species, I selected at random one or two recordings from a particular recording period; two were included only if the time interval exceeded 60 min. Since the species composition and especially the size of the dabbling duck feeding groups varied considerably from one recording to another, this criterion seems strict enough to ensure that the feeding groups included were reasonably independent. All in all, 93 % of the recordings (N = 483) were used in analyses of group size, 68 % in analyses of species number and 27 % in tests of the association and correlation in individual numbers between two species.

The association (positive or negative) between two species was measured with the coefficient of association suggested by Cole (1949, after Pielou 1977). The three versions of Cole's coefficient used were (note that the parameter symbols are partly different from those of Pielou 1977):

$$C = \frac{ad-bc}{(a+b)(b+d)}$$

in the case of positive association (i.e. ad > bc) and

$$C = \frac{ad-bc}{(a+b)(a+c)}, \text{ if } a \leq d, \text{ or } C = \frac{ad-bc}{(c+d)(b+d)}$$

if a > d, in the case of negative association (i.e. ad < bc). The parameters are: a = both species present, b = only species 1 present, c = only species 2 present, and d = neither species present. The value of C ranges from –1 (maximum negative association) to + 1 (maximum positive association), and 0 means no association at all.

The feeding depths of the species were calculated using data on the feeding methods and morphology (body length, neck length, skull length, bill length) (Fig. 1; see also Pöysä 1983b, 1986).

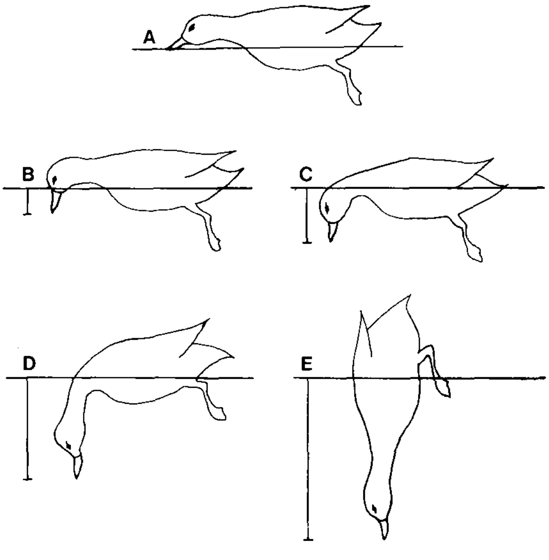

Fig. 1. Schematic presentation of feeding methods and depths of dabbling ducks. A = picking/straining from surface, B = bill submerged, C = head submerged, D = neck submerged and E = up-ending. Vertical bars give the maximum feeding depth used in calculations; for picking/straining from surface 1 cm was used for all species.

Results

Species number and size of the feeding groups. Two-, three- and one-species groups were the most frequent, with proportions of 31.3 %, 28.2 % and 25.2 %, respectively (N = 326). The Teal *Anas crecca* and Shoveler *A. clypeata* were the most frequent species in both one-species and mixed groups, the least frequent species in one-species groups being the Garganey *A. querquedula* and the Pintail *A. acuta* (Table 1). The rank order of the frequencies of the six species in mixed groups correlates significantly with the ranking in abundance ($r_s = 0.943$, $P < 0.05$), but in one-species groups the corresponding correlation, albeit strong, is marginally not significant ($r_s = 0.886$, $P < 0.10$). In the Mallard *A. platyrhynchos* the number of one-species groups is significantly greater than could be expected on the basis of its relative abundance in the groups ($\chi^2 = 6.13$, $P < 0.05$) and in the Teal the reverse is true ($\chi^2 = 4.74$, $P < 0.05$). In the other species the difference between the observed and expected numbers of one-species groups is not significant. A comparison between the proportions of observations of one-species and mixed groups in the total observations of a particular species suggests that none of the species preferred foraging in one-species groups to foraging in mixed groups (Table 1).

The 449 feeding groups included in the group size analysis were divided among five size classes, according to the number of individuals: 1–10 (61.0 % of all groups), 11–20 (20.9 %), 21–30 (9.6 %), 31–40 (4.0 %) and > 40 (4.5 %) individuals. The mean size of the groups was 12.5 (SD = 13.2) and the median 8.0 individuals. The Teal was clearly the most numerous in these groups (Table 2). There were differences between the species in frequency and the mean number of individuals in the size classes (Table 2). Only in the Teal did both the frequency and mean number increase consistently with group size. The Garganey and Pintail occurred most frequently in the largest groups, but their mean numbers varied without clear trends among the group size classes. The Mallard, Wigeon *A. penelope* and Shoveler occurred most frequently in some intermediate group size class; the mean number of Mallards was greatest in the second size class and the numbers of Wigeons and Shovelers were greatest in the largest class.

Association and correlation in individual number between species. The total numbers of positive and negative associations between two species were 7 and 8, respectively (Table 3). However, only between the Teal and Garganey was there a significant positive association and between the Garganey and Wigeon a significant negative association. In 3 of the 15 species pairs the individual numbers had a significant positive correlation, viz. between the Teal and Shoveler, Garganey and Pintail, and Garganey and Shoveler (Table 3).

Group size and feeding depth of the species. The average feeding depths of the species varied to some degree between the five feeding group size classes (Fig. 2). In some species the feeding depth tended to be great in both the smallest and largest feeding groups and small (i.e. near water surface) in the medium-sized groups the minimum depth being located in different group size classes in different species. However, when differences in the feeding depth between the first and the "minimum" group size class and between the last and the "minimum" group size class were tested for each species, a significant increase in the feeding depth with group size was found only in the Teal (Mann-Whitney U-test, $z = 4.18$, $P < 0.001$) and in the Shoveler (Mann-Whitney U-test, $z = 2.96$, $P < 0.01$). In contrast to the other species, the Teal had virtually the same average feeding depth in the first four group size classes (Fig. 2).

Table 1. Frequencies and relative abundances (%) of the dabbling ducks in the 326 one-species and multispecies feeding groups.

	Frequency		Relative abundance in all groups (4007 ind.)	Proportion (and total number) of observations of each species	
	one-species groups (N = 82)	multispecies groups (N = 244)		one-species groups	multispecies groups
Mallard, *Anas platyrhynchos*	13.4	36.6	6.5	10.9 (101)	89.1
Teal, *A. crecca*	40.2	75.7	58.6	15.1 (218)	84.9
Garganey, *A. querquedula*	6.1	37.9	5.1	5.1 (98)	94.9
Wigeon, *A. penelope*	12.2	38.7	11.2	9.5 (105)	90.5
Pintail, *A. acuta*	8.5	25.9	4.9	9.9 (71)	90.1
Shoveler, *A. clypeata*	19.5	65.8	13.6	9.0 (177)	91.0

Table 2. Mean numbers of the dabbling duck species in the 449 feeding groups and their frequencies (A) and mean numbers (B) in groups of different sizes. N = number of groups in which each species occurred.

	N	$\bar{X}$	Group size classes									
			1—10		11—20		21—30		31—40		> 40	
			A(%)	B($\bar{X}$)	A	B	A	B	A	B	A	B
Mallard	133	2.9 (SD = 2.9)	26.3	2.2 (1.6)	27.7	4.7 (4.1)	44.3	3.6 (4.2)	50.0	1.9 (0.7)	30.0	1.8 (0.7)
Teal	309	11.0 (12.4)	52.9	3.2 (2.3)	88.3	9.5 (5.2)	100.0	17.7 (6.1)	100.0	26.0 (6.2)	100.0	45.2 (13.8)
Garganey	129	2.2 (1.8)	20.1	1.8 (1.3)	38.3	2.4 (1.9)	39.5	1.9 (1.5)	50.0	3.7 (2.7)	60.0	2.4 (1.9)
Wigeon	133	4.3 (3.6)	25.9	3.0 (2.3)	25.5	5.1 (3.5)	55.8	4.8 (3.1)	44.4	5.8 (4.0)	30.0	12.7 (3.0)
Pintail	96	2.8 (2.4)	19.3	2.0 (1.6)	23.4	4.2 (2.8)	18.6	2.4 (2.3)	27.8	3.4 (1.9)	40.0	4.3 (3.1)
Shoveler	234	3.0 (2.3)	42.0	2.5 (1.7)	69.1	3.2 (2.4)	62.8	2.5 (2.1)	77.8	3.7 (2.1)	60.0	6.8 (3.6)

Table 3. Association (C, with χ^2 tests for statistical significance) and correlation between individual numbers (r) for each species pair in the 131 randomly selected feeding groups. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. For further explanations see Material and methods.

Species 1	2	C	χ^2		r	
Mallard	Teal	−0.12	1.79	ns	−0.106	ns
Mallard	Garganey	−0.11	0.43	ns	−0.038	ns
Mallard	Wigeon	+0.07	0.75	ns	0.062	ns
Mallard	Pintail	−0.22	1.00	ns	−0.094	ns
Mallard	Shoveler	−0.02	0.03	ns	−0.154	ns
Teal	Garganey	+0.11	7.25	**	0.027	ns
Teal	Wigeon	−0.08	0.76	ns	0.103	ns
Teal	Pintail	+0.01	0.07	ns	0.053	ns
Teal	Shoveler	+0.02	0.08	ns	0.319	***
Garganey	Wigeon	−0.54	8.29	**	−0.169	ns
Garganey	Pintail	+0.08	1.28	ns	0.236	**
Garganey	Shoveler	+0.12	0.64	ns	0.172	*
Wigeon	Pintail	−0.35	2.09	ns	−0.143	ns
Wigeon	Shoveler	+0.02	0.02	ns	0.023	ns
Pintail	Shoveler	−0.06	0.19	ns	0.107	ns

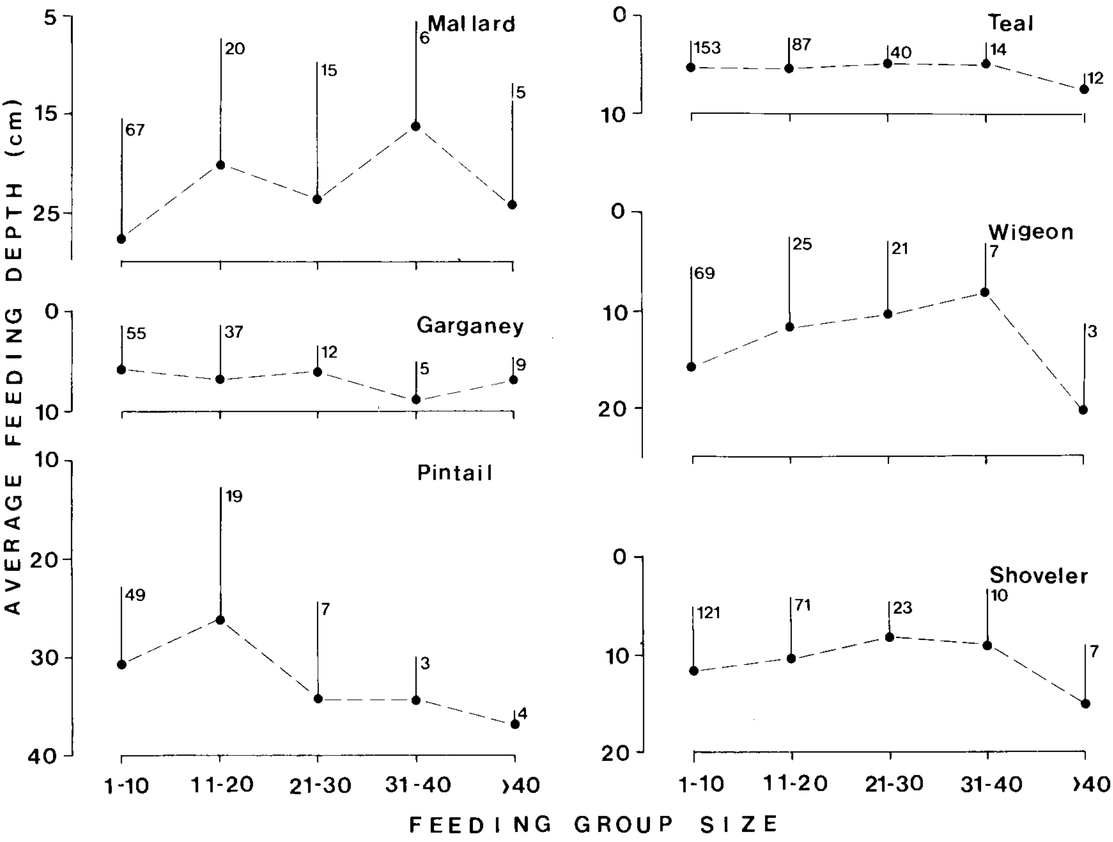

Fig. 2. Average feeding depths of the dabbling duck species in groups of different size classes. The vertical bars represent 1 SD and the numbers of feeding groups are given to the right of them.

Group size and spatial use in the Teal and Shoveler. The increase in the feeding depth observed in the Teal and Shoveler may be due to greater use of less profitable (e.g. submerged vegetation at greater depth) parts of the feeding area in very large groups. I tested this as follows. The feeding area used here was divided into 24 feeding sectors in Pöysä (1986; note that only data from 1982 were used). Using the primary data from that study pooled over groups greater than or equal in size to the "minimum" size class, I calculated both for the Teal and the Shoveler the percentage use of each of the 24 feeding sectors. I then grouped the sectors into two categories for each species: percentage use I) greater or II) smaller than the average percentage use of all sectors (null sectors excluded). If the hypothesis proposed above is correct, the proportional use of the feeding sectors belonging to category II) (indicating less profitable sectors here) should be greater in groups greater than the "minimum" group size class than the use in the "minimum" class. This was true in the Teal but not in the Shoveler (Table 4).

Changes in feeding depth during the time spent foraging in a group. To check whether there were any consistent changes in the average feeding depth of the species during the recording periods, I calculated the average feeding depth for each species at each recording (the concepts of recording period and recording explained in Material and methods). I am here interested only in the question whether the feeding depth of a species does, or does not, shift from the surface layer toward the bottom from the first to the last recording in a recording period. Consequently, I used for each species only recording periods in which the average feeding depth of the species was 1–10 cm at the first recording. The results for species with sufficient data are shown in Table 5. In the Teal the number of recording periods during which an increase in the feeding depth was observed is significantly greater than the number of recording periods in which no such trend was found (i.e. it remained the same or decreased). The mean group size seemed to be greater during the recording periods that showed an increasing trend in the feeding depth than during the periods without any such trend (Table 5). This was the case in the Wigeon and Shoveler too.

Table 4. Percentage use of feeding sectors belonging to categories I and II in the Teal and Shoveler in the "minimum" group size class and in groups greater than this. For further explanations see text.

	Teal		Shoveler	
Category:	I	II	I	II
"Minimum" group size class	93.3	6.7	75.0	25.0
	$\chi^2 = 9.04, P < 0.01$		$\chi^2 = 4.42, P < 0.05$	
Groups > "minimum" class	78.5	21.5	86.7	13.3

Discussion

Species interaction and the composition and size of the feeding groups. In some species pairs, the results regarding association and correlation between individual numbers suggested that interspecific interactions may contribute to structure the dabbling duck feeding groups. Here, I am interested in competition for food resources as a possible harmful species interaction in mixed groups (e.g. Morse 1970, Alerstam et al. 1974, Wiley 1980, Alatalo 1981, Alatalo et al. 1985), and in facilitation of food-finding by copying the foraging behaviour of other species as a possible beneficial interaction (e.g. Krebs 1973, Rubenstein et al. 1977, Greig-Smith 1978, Caldwell 1981). If competition for food resources occurs, those species that overlap more in their foraging niches should compete more strongly than species that overlap less (for recent reviews, see Schoener 1982, 1983). On the other hand, if beneficial interaction occurs instead of competition, we may expect that species most similar in foraging behaviour should benefit most in food-finding from one another's presence (see also Krebs 1973, Herrera 1979).

In the context of this paper the above predictions would imply that, if competitive interactions prevail, dabbling duck species that are most similar in terms of feeding site, method and depth (see Pöysä 1986)

Table 5. Changes in feeding depth of the Teal, Garganey, Wigeon and Shoveler (species with enough data) during recording periods. A = number of recording periods in which the feeding depth increased from the first recording to the last, B = number of recording periods without an increase in the feeding depth. The change in the feeding depth during each recording period was checked by calculating a correlation coefficient (statistical significance ignored) between the average feeding depth at a given recording and the time elapsed between the recording and the beginning of the recording period. The mean group sizes during both types (A and B) of recording periods are also given.

		χ^2		Mean group size
Teal	A 33	5.12	$p < 0.05$	20.6 (SD = 14.2)
	B 17			11.0 (7.3)
Garganey	A 11	–	–	17.3 (14.1)
	B 11			17.9 (12.4)
Wigeon	A 7	0.08	$p > 0.75$	17.5 (11.9)
	B 6			11.9 (6.2)
Shoveler	A 16	0.31	$p > 0.50$	18.9 (15.4)
	B 13			12.0 (7.3)

should be most clearly negatively associated and/or have highest negative correlations between their individual numbers; in the case of beneficial interaction, the reverse should be true. The correlations calculated to test this were not significant and do not support the prediction (Table 6; for foraging niche similarities see Appendix). Considering niche shifts along the same foraging niche dimension among the species (see Pöysä 1986), we may further predict that two species showing the greatest divergent niche shift (possible harmful interaction) should be the most clearly negatively associated species and/or should have the highest negative correlation between their individual numbers, and that two species showing the strongest convergent shift (possible beneficial interaction) should show the opposite relations. This was, however, not the case (Table 6). Consequently, as no significant support for the interaction hypotheses was found here either, I suggest that interspecific foraging interactions do not consistently explain the species composition or the numerical relations among the species in the dabbling duck feeding groups studied.

As the results of this study and of Pöysä (1986) relate to the species composition, size and foraging ecology of feeding groups in a small feeding area, it is difficult to make comparisons with results from population-level studies. However, as in this study, no consistent evidence of competitive species interaction was derived from analyses of the spatial and temporal dynamics of breeding dabbling duck populations in Siikalahti (Pöysä 1984a) or from analyses of the species composition of local breeding dabbling duck assemblages in different parts of Finland (Pöysä 1984b).

Some species pairs deserve a little further discussion. Significant positive association or positive correlation between individual numbers was found in the species pairs Teal and Garganey, Teal and Shoveler, and Garganey and Shoveler. In all these pairs beneficial interaction was also suggested in the niche shift analyses, the species being very similar in their general foraging ecology and behaviour (Pöysä 1983a, 1986). Taken together, these observations give strong empirical support for beneficial interaction among foraging Teals, Garganeys and Shovelers (but for possible harmful interaction between the Teal and Shoveler see Pöysä 1985). The spatio-temporal population dynamics was similar among these three species in Siikalahti (Pöysä 1984a, Fig. 3) and positive association in occupation of different lakes was suggested especially between the Garganey and Shoveler (Pöysä 1984b). The Garganey was significantly negatively associated with the Wigeon and had a significant positive correlation in individual number with the Pintail. Unfortunately data on niche shifts in these pairs were not available, but as foraging niche overlaps between these species are not very great, foraging interactions may not have been involved. It should be mentioned, however, that population-level studies gave some indication of positive association between the Garganey and Pintail (see Pöysä 1984a, b).

Limits to the size of the feeding groups. Large groups were only occasionally observed. However, at most times the total number of dabbling ducks present in the whole study area (Siikalahti) was much greater than that recorded foraging in the feeding patch studied here. What factors may have limited the size of the feeding groups? The increase in the feeding depth with group size observed in the Teal and Shoveler, and possibly in some other species too, may have two explanations. First, as all parts of the feeding patch studied may not be equally profitable in terms of feeding depth for dabbling ducks, it is possible that in very large groups, some individuals were forced to forage in marginal sites, at greater feeding depths. Second, the density of food at or near the water surface may have decreased markedly with an increase in group size. Support for the first hypothesis was found in the Teal but not in the Shoveler. The effects of group size on the spatial use of a feeding patch are presumably stronger intra- than interspecifically. As the Teal was much more numerous in the largest groups (Table 2), it is possible that the most profitable feeding sites were filled and some individuals were forced to forage in margi-

Table 6. Relationship (r) of the species associations and correlation coefficients between individual numbers to similarities and magnitudes of niche shifts along different foraging niche dimensions. N = number of species pairs in each comparison. For species associations and correlations between individual numbers see Table 3 and for foraging niche overlaps and shifts see Appendix.

	Overlap in feeding		Ratio in	Magnitudes of niche shifts in feeding		
	site	method	feeding depth	site	method	depth
Association vs.	0.210 ns	0.301 ns	0.044 ns	0.035 ns	0.115 ns	–0.361 ns
Correlation between individual numbers vs.	0.211 ns	0.104 ns	0.190 ns	0.202 ns	0.092 ns	0.093 ns
N	15	15	15	11	12	12

nal sites. Increased use of less suitable feeding areas with increasing bird density has also been reported from the wintering areas of the Teal (Zwarts 1976). By contrast, in the Shoveler, the intraspecific pressure to use marginal feeding sites was not so great. Consequently, the second explanation proposed above is the more probable, at least for the Shoveler.

The density of food near the water surface may have been decreased both by depletion, the food being removed by the ducks, and by disturbance, the animal prey moving toward the bottom and/or hiding in vegetation. It has been demonstrated that predation may have an impact on the abundance and behaviour of aquatic invertebrates (e.g. Sih 1979, 1982, Crowder & Cooper 1982, Cook & Stream 1984). The frequent increase in the feeding depth of the Teal with time spent foraging in the patch supports the assumption that the surface layer became less profitable to the ducks. During 16 of the 33 recording periods that showed an increasing trend in the feeding depth of the Teal, the group size simultaneously decreased (checked from primary data). This suggests that density-dependent spatial use of the feeding area (the first explanation above) is not the only factor accounting for increased feeding depth in the Teal either. Since the number of ducks foraging and moving around was often great, both depletion and disturbance were probably notable. Similarly, Goss-Custard (1976, 1980) observed that the rate of food intake by wading birds may decrease as the bird density at the feeding site increases. He pointed out that as the bird density increases, the prey is more heavily depleted and also retreats more into the mud. A similar phenomenon was suggested by Waite (1984) in large feeding associations of corvids. As regards interspecific interactions, the prey disturbance suggested here (see also Pöysä 1985) corresponds to the passive interference considered by Maurer (1984; see also Charnov et al. 1976); direct aggression is rare, but interaction occurs via resource depression caused by the foraging of coexisting species.

Feeding in large groups may thus involve costs in the sense that the ducks are compelled to use time- and energy-consuming feeding methods. It is intuitively obvious that, other things being equal, for example the feeding method of up-ending is much more energy-consuming than feeding with the bill submerged. Moreover, up-ending reduces vigilance, whereas a duck feeding with only the bill submerged can still scan its environment for predators and for neighbouring individuals (Pöysä, in prep.). This may be important, because feeding and vigilance are conflicting demands in the time budgeting of foraging birds of many species (e.g. Caraco 1979, Lendrem 1983, Metcalfe & Furness 1984).

Why was the feeding depth of some species so great even in the smallest feeding groups? In general, there is a positive relationship between food density and bird density or feeding group size (e.g. Goss-Custard 1970, Kushlan 1976, Barnard 1980, Birkhead & Furness 1984). As the mean number of Teals, almost exclusively surface-feeders (see Pöysä 1983a, b, 1986), was small in the smallest feeding group size class, it is possible that food density was not high at the surface layer in these groups. If this was true, then it would not pay for the larger dabbling duck species, which need more food and can feed at greater depths, to use the surface layer, and their feeding depths were thus great. This argumentation is supported by the observations of Danell & Sjöberg (1982). They found that when changes in the weather reduced the abundance of food at the water surface, fewer Teals foraged in the same water area and those present either did or did not increase feeding below the water surface. Similar changes were observed in the Mallard and Pintail (Danell & Sjöberg 1982, Figs 2a–c). The greater numbers of Teals in the larger feeding group size classes may have indicated improvement in food resources. This could explain the tendency of some species to shift the feeding depth toward the water surface in the intermediate group size classes.

When the frequencies of each species in the feeding group size classes are compared with the feeding depth, no consistent support can be found for the assumption that each species forages more frequently in groups in which its feeding depth is smallest. The feeding depth is thus by no means the only factor accounting for the patterns of occurrence of the species in the mixed groups. I suggest, however, that an increase in the feeding depth due to the reasons suggested above is important in limiting the size of the feeding groups and explains why large groups were so rare.

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Selostus: **Puolisukeltajasorsien ruokailuparvien lajikoostumus ja koko**

Puolisukeltajasorsien ruokailuryhmien lajikoostumusta ja kokoa tutkittiin Parikkalan Siikalahdella kesinä 1980, -82 ja -83. Tavoitteena oli selvittää vaikuttavatko lajien väliset, ruokailuekologiaan ja -käyttäytymiseen liittyvät suhteet lajien esiintymiseen ja yksilömääriin parvissa. Lisäksi tutkittiin tekijöitä, jotka mahdollisesti rajoittavat ruokailuparvien kokoa yleensä.

Parvet koostuivat useimmin 1–3 lajista (maksimi 6), joista yleisimmin esiintyvät lajit olivat tavi ja lapasorsa (taul. 1). Yksilömäärältään runsain laji oli tavi ja vähälukuisin heinätavi (taul. 2). Joidenkin lajien välillä oli tilastollisesti merkitsevä positiivinen tai negatiivinen assosiaatio ja joidenkin lajien yksilömäärät parvissa korreloivat merkitsevän positiivisesti keskenään (taul. 3). Kun näitä tuloksia verrattiin aiemmin saatuihin lajien samankaltaisuuksiin ja vuorovaikutuksiin ruokailupaikan, -tavan ja -syvyyden suhteen havaittiin, että lajien ruokailuekologiaan ja -käyttäytymiseen liittyvät vuorovaikutussuhteet eivät johdonmukaisesti selitä ruokailuparvien lajikoostumusta ja lajien keskinäisiä runsaussuhteita (taul. 6). Kolmessa lajiparissa vertailut viittaavat kuitenkin vahvasti positiivisen vuorovaikutuksen esiintymiseen lajien välillä.

Joidenkin lajien ruokailusyvyys kasvoi selvästi hyvin suurissa ryhmissä keskikokoisiin ryhmiin verrattuna (kuva 2). Tämän oletetaan johtuvan kahdesta tekijästä: suurissa ruokailuryhmissä jotkut yksilöt joutuvat ruokailemaan heikommilla (syvyys uposkasvillisuuteen mahdollisesti suurempi) ruokailupaikoilla ja/tai ravintotilanne lähellä pintaa heikkenee voimakkaasti sorsien ruokailun ja siitä aiheutuvan häirinnän vuoksi. Näiden tekijöiden oletetaan rajoittavan tietyllä ruokailulaikulla ruokailevan puolisukeltajaparven kokoa.

References

Alatalo, R. V. 1981: Interspecific competition in tits Parus spp. and the goldcrest Regulus regulus: foraging shifts in multispecific flocks. — Oikos 37:335–344.

Alatalo, R. V., Gustafsson, L., Lindén, M. & Lundberg, A. 1985: Interspecific competition and niche shifts in tits and the goldcrest: an experiment. — J. Anim. Ecol. 54:977–984.

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

Barnard, C. J. 1980: Factors affecting flock size mean and variance in a winter population of house sparrows (Passer domesticus L.). — Behaviour 74:114–127.

Barnard, C. J. & Stephens, H. 1981: Prey size selection by lapwings in lapwing/gull associations. — Behaviour 77:1–22.

Barnard, C. J., Thompson, D. B. A. & Stephens, H. 1982: Time budgets, feeding efficiency and flock dynamics in mixed species flocks of lapwings, golden plovers and gulls. — Behaviour 80:44–69.

Bertram, B. C. R. 1978: Living in groups: predators and prey. — *In* Krebs, J. R. & Davies, N. B. (eds.): Behavioural ecology: an evolutionary approach, pp. 64–96. — Blackwell, Oxford.

Birkhead, T. R. & Furness, R. W. 1985: Regulation of seabird populations. — *In* Sibly, R. M. & Smith, R. H. (eds.): Behavioural ecology: ecological consequences of adaptive behaviour, pp. 145–167. — Blackwell, Oxford.

Caldwell, G. S. 1981: Attraction to tropical mixed-species heron flocks: proximate mechanism and consequences. — Behav. Ecol. Sociobiol. 8:99–103.

Caraco, T. 1979: Time budgeting and group size: a test of theory. — Ecology 60:618–627.

Charnov, E. L., Orians, G. H. & Hyatt, K. 1976: Ecological implications of resource depression. — Am. Nat. 110:247–259.

Cole, L. C. 1949: The measurement of interspecific association. — Ecology 30:411–424.

Cook, W. L. & Streams, F. A. 1984: Fish predation on Notonecta (Hemiptera): relationship between prey risk and habitat utilization. — Oecologia (Berl.) 64:177–183.

Crowder, L. B. & Cooper, W. G. 1982: Habitat structural complexity and the interaction between bluegills and their prey. — Ecology 63:1802–1813.

Danell, K. & Sjöberg, K. 1982: Seasonal and diel changes in the feeding behaviour of some dabbling duck species on a breeding lake in northern Sweden. - Ornis Scand. 13:129–134.

Goss-Custard, J. D. 1970: The responses of Redshank (Tringa totanus (L.)) to spatial variations in the density of their prey. — J. Anim. Ecol. 39:91–113.

Goss-Custard, J. D. 1976: Variation in the dispersion of Redshank Tringa totanus on their winter feeding grounds. — Ibis 118:257–263.

Goss-Custard, J. D. 1980: Competition for food and interference among waders. — Ardea 68:31–52.

Goss-Custard, J. D., Durell, S. E. A. le V. dit, McGrorty, S. & Reading C. J. 1982: Use of mussel Mytilus edulis beds by oystercatchers Haematopus ostralegus according to age and population size. — J. Anim. Ecol. 51:543–554.

Greig-Smith, P. W. 1978: Imitative foraging in mixed-species flocks of Seychelles birds. — Ibis 120:233–235.

Herrera, C. M. 1979: Ecological aspects of heterospecific flocks formation in a Mediterranean passerine bird community. — Oikos 33:85–96.

Hoffman, W., Heinemann, D. & Wiens, J. A. 1981: The ecology of seabird feeding flocks in Alaska. — Auk 98:437–456.

Krebs, J. R. 1973: Social learning and the significance of mixed-species flocks of chickadees (Parus spp). — Can. J. Zool. 51:1275–1288.

Kushlan, J. A. 1976: Site selection for nesting colonies by the American White Ibis Eudocimus albus in Florida. — Ibis 118:590–593.

Lendrem, D. W. 1983: Predation risk and vigilance in the blue tit (Parus caeruleus). — Behav. Ecol. Sociobiol. 14:9–13.

Maurer, B. A. 1984: Interference and exploitation in bird communities. — Wilson Bull. 96:380–395.

Metcalfe, N. B. & Furness, R. W. 1984: Changing priorities: the effect of pre-migratory fattening on trade-off between foraging and vigilance. — Behav. Ecol. Sociobiol. 15:203–206.

Moriarty, D. J. 1976: The adaptive nature of bird flocks: a review. — Biologist 58:67–79.

Morse, D. H. 1970: Ecological aspects of some mixed-species foraging flocks of birds. — Ecol. Monogr. 40:119–168.

Morse, D. H. 1977: Feeding behaviour and predator avoidance in heterospecific groups. — BioSci. 27:332–339.

Pielou, E. C. 1977: Mathematical ecology. — John Wiley & Sons, New York, London.

Pulliam, R. H. & Millikan, G. C. 1982: Social organization in the non-reproductive season. — *In* Farner, D. S. & King, J. R. (eds.): Avian biology Vol VI, pp. 169–197. — Academic Press, New York.

Pulliam, R. H. & Caraco, T. 1984: Living in groups: is there an optimal group size? — *In* Krebs, J. R. & Davies, N. B. (eds.): Behavioural ecology: an evolutionary approach, 2nd ed., pp. 122–147. — Blackwell, Oxford.

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

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

Pöysä, H. 1983c: Parikkalan Siikalahden vesilinnuston rakenteesta ja alueellisesta vaihtelusta suhteessa ympäristön rakenteeseen (Summary: The structure of a waterfall community in relation to habitat structure in SE Finland). — Suomen Riista 30:5–14.

Pöysä, H. 1984a: Temporal and spatial dynamics of waterfowl populations in a wetland area — a community ecological approach. — Ornis Fennica 61:99–108.

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

Pöysä, H. 1985: Circumstantial evidence of foraging interference between two species of dabbling ducks. — Wilson Bull. 97:541–543.

Pöysä, H. 1986: Foraging niche shifts in multispecies dabbling duck (Anas spp.) feeding groups: harmful and beneficial interaction between species. — Ornis Scand., in press.

Rubenstein, D. I., Barnett, R. J., Ridgely, R. S. & Klopfer, P. H. 1977: Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. — Ibis 119:10–21.

Schoener, T. W. 1982: The controversy over interspecific competition. — Am. Sci. 70:586–595.

Schoener, T. W. 1983: Field experiments on interspecific competition. — Am. Nat. 122:240–285.

Sih, A. 1979: Stability and prey behavioural responses to predator density. — J. Anim. Ecol. 48:79–89.

Sih, A. 1982: Foraging strategies and the avoidance of predation by an aquatic insect, Notonecta hoffmanni. — Ecology 63:786–796.

Waite, R. K. 1984: Sympatric corvids. Effects of social behaviour, aggression and avoidance on feeding. — Behav. Ecol. Sociobiol. 15:55–59.

Wiley, R. H. 1980: Multispecies antbird societies in lowland forests of Surinam and Ecuador: stable membership and foraging differences. — J. Zool. Lond. 191:127–145.

Zwarts, L. 1976: Density-related processes in feeding dispersion and feeding activity of Teal (Anas crecca). — Ardea 64:192–209.

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Appendix. Foraging niche similarities and magnitudes of foraging niche shifts between dabbling duck species. Overlaps in feeding site and method are derived from Pöysä (1986, Table 1; overalls have been used here). Ratios (larger to smaller) in feeding depths are calculated using the average feeding depth values given by Pöysä (1986, section 3.3). Magnitudes of niche shifts in terms of feeding site, method and depth are calculated on the basis of overlaps when the two species have been foraging separately and together (overlaps are given in Pöysä 1986, Table 1) by dividing the difference between foraging separately and together by the overlap when the species have been foraging separately; plus signs mean convergent and minus signs divergent niche shifts.

		Overlap in feeding		Ratio in feeding	Magnitudes of niche shift in feeding		
		site	method	depth	site	method	depth
Mallard	vs. Teal	0.52	0.55	4.2	+ 0.02	–0.58	–0.12
Mallard	vs. Garganey	0.52	0.59	3.3	–0.03	–	–
Mallard	vs. Wigeon	0.20	0.58	1.3	–0.45	–0.03	–2.08
Mallard	vs. Pintail	0.57	0.64	1.4	–	+ 0.93	+ 0.42
Mallard	vs. Shoveler	0.58	0.69	1.7	–0.08	–0.35	–0.86
Teal	vs. Garganey	0.50	0.90	1.3	–	+ 0.17	+ 0.15
Teal	vs. Wigeon	0.31	0.41	3.3	–0.26	–0.33	–0.34
Teal	vs. Pintail	0.52	0.22	6.0	+ 0.30	+ 14.25	+ 0.44
Teal	vs. Shoveler	0.74	0.82	2.4	+ 0.21	+ 0.28	+ 0.31
Garganey	vs. Wigeon	0.41	0.41	2.6	–	–	–
Garganey	vs. Pintail	0.33	0.29	4.7	–	–	–
Garganey	vs. Shoveler	0.57	0.88	1.9	+ 0.14	–0.04	+0.22
Wigeon	vs. Pintail	0.18	0.47	1.8	+ 0.07	–0.36	+ 0.52
Wigeon	vs. Shoveler	0.36	0.43	1.4	+ 0.72	–0.26	–1.45
Pintail	vs. Shoveler	0.51	0.39	2.5	+ 1.10	+ 1.61	+ 0.48