

High overlap in diets of sympatric dabbling ducks — an effect of food abundance?

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We studied diet patterns of six sympatric dabbling ducks (*Anas* sp.) in wetlands with abundant invertebrates. In contrast to some earlier studies, we found no correlation between the lamellar density of different ducks and the mean length of prey in their diet. The size distributions of prey in the diet of different ducks varied, however, although in most cases the differences were not very large. Compared with earlier studies, the prey size distributions in the diet of the ducks differed quite little from that in the environment. There was not much segregation of food use along the vertical foraging dimensions, although teal *Anas crecca* and wigeon *Anas penelope* used invertebrates above the water surface. We propose that the high level of diet overlap was promoted by abundant food resources, which are quite typical for habitats where many species of dabbling ducks coexist.

Introduction

In the context of interspecific competition, resource abundance is considered to affect the way in which coexisting members of a same guild will use it. High diet overlap, for example, is often linked with “fat” times, with abundant food, and low diet overlap with “lean” times (Smith *et al.* 1978, Schoener 1986, Wiens 1989, but *see* Pulliam 1985, Wiens 1993). Opportunism in food use may also be promoted by environmental variability, which prevents the species from fine-tuning to their competitive milieu (Rotenberry 1980). The form of change in resource levels may

also influence how overlap changes (Nudds 1992). If food availability decreases over the entire size spectrum, potential competitors may diverge in resource use; an uneven reduction that leaves some resource types relatively abundant may lead to greater overlap in food use (Grant & Grant 1980, Wiens 1989).

Dabbling ducks (*Anas* spp.) form a compact foraging guild in waterfowl assemblages (Pöysä 1983a, Pöysä *et al.* 1994). In dabbling duck food partitioning, the importance of differences in bill lamellar densities (Nudds & Bowlby 1984, Nudds *et al.* 1994), neck length (Pöysä 1983b, Pöysä *et al.* 1994) and foraging behaviour (Pöysä 1987,

Nummi 1993) has been stressed, as well as the effect of habitat structure on the importance of these different factors (Nudds *et al.* 2000).

Bill lamellar density is associated with the size of prey taken by the ducks of different species (Nudds & Bowlby 1984, Nummi 1993), and can, therefore, lead to microhabitat segregation among the species. In Nearctic prairie wetlands (and also in shallow Baltic wetlands), ducks with coarse lamellae foraged in inshore, well-vegetated habitats, whereas ducks with fine lamellae searched for food in open, offshore habitats (Nudds 1992, Nudds *et al.* 1994). This reflects the gradient of size distributions of invertebrates found in North American prairie potholes (Armstrong & Nudds 1985).

There has, however, been some discussion about the generality of this habitat-partitioning pattern (Pöysä *et al.* 1994, 1996, Nudds *et al.* 2000). In studies conducted in Nordic inland lakes, the species with longer bodies but with coarse lamellae tend to prefer the deeper, more open waters, whereas those with shorter bodies and fine lamellae prefer vegetated habitats (Pöysä *et al.* 1996, *see also* Euliss & Harris 1987). Likewise, the duck guilds of northern Europe seem to assemble according to differences in body size rather than differences in bill lamellar density (Pöysä *et al.* 1994). The diets of sympatric teal *Anas crecca* and mallard *A. platyrhynchos* have also been found to differ clearly along the vertical axis (depth) of the foraging habitats (Nummi 1993), reflecting the feeding methods used by the two species (Pöysä 1983b).

Here we report the invertebrate diet patterns of dabbling ducks in a habitat with abundant invertebrates, comparing directly the feeding niches of six dabbling ducks from the same lakes from which the prey availability data were collected. We focus especially on the size distributions of prey in the diets of different ducks, and on the association of bill lamellar density and mean prey size in the diet.

Study area and methods

Our study area consisted of a complex of three permanent interconnected eutrophic lakes with similar hydrology in the central part of Finland

(63°N, 27°E). The lakes are mostly surrounded by cultivated fields and the size of the lakes is 0.4, 0.7 and 2.0 km². The largest lake in our study area was Lapinjärvi, where most of the data were collected. The total study area was about 5 km². Emergent vegetation covered about 40% of the total lake area; the dominant stands were formed by sedges *Carex* spp. and horsetails *Equisetum fluviatile*. Reed *Phragmites australis* and bull-rush *Shoenoplectus lacustris* were also abundant. All lakes had fish populations.

Data were collected in 1992–1998. For diet studies, ducks were collected during post-breeding period between August 20 (beginning of the hunting season) and the end of September. The esophagi were removed after shooting and preserved in alcohol (Swanson & Bartonek 1970). The volume of different food items was measured by liquid displacement, and the data were summarized as aggregate percentages within each duck species (Swanson *et al.* 1974). Prey types in the esophagi were assigned to the same four length classes that were used in assessing the availability of invertebrates in the environment (Nudds & Bowlby 1984, Nummi 1993; *see below*). We have prey data from six dabbling ducks, all of which also breed in our study area. For some species, sample size is quite small. However, because of the often limited numbers of individuals of rare species present locally, this is not unusual for studies of sympatric collection of birds (e.g. Rotenberry 1980, DuBowy 1988). Prey size distributions of the duck species were compared with each other and with the prey size distribution in the environment with *G*-tests. Because size distributions are based on percentages, *G*-values are used as an index of relative difference between the prey size distributions (Nudds & Bowlby 1984, Nummi 1993, Nummi *et al.* 1995). When correlating the average prey size in the diet of each duck species with bill lamellar density, we used lamellar density values given in Nudds *et al.* (1994).

We focused only on invertebrates because of two reasons. First, invertebrate protein is essential to all ducks during breeding and moulting (Hohman *et al.* 1992, Sedinger 1992), therefore even small amounts of invertebrates are important; the nutritive value of invertebrates and plants is so different that considering them to-

gether is not biologically sound (Street 1978, Krapu 1979). Second, present knowledge of predator-prey size relationships in dabbling ducks is largely based on a single literature study, where the birds were collected from different parts of North America (Nudds & Bowlby 1984). In order to add to the knowledge of the organization of dabbling duck communities, we consider it important to be able to compare the pattern found in our sympatrically collected birds with that in earlier studies (Nudds & Bowlby 1984, Nummi 1993).

To study the vertical distribution of prey in the diets, the invertebrates were assigned to three classes according to their usual position in aquatic habitats: living on or above the water surface, nektonic, and living on the bottom or otherwise attached to underwater surfaces (Mellanby 1951, Nummi 1993). Vertical distribution of prey should reflect foraging habitat partitioning along the vertical axis (Pöysä *et al.* 1994).

In availability-use patterns of duck diet studies, the availability-data have usually been based on either corer, sweep-net or activity trap samples (Mittelbach 1981 in Nudds & Bowlby 1984, Nummi 1993, Nummi *et al.* 1995). Different devices may, however, give a slightly different picture of the available prey (Elmberg *et al.* 1992, Hyvönen & Nummi 2000). Therefore, both activity traps and corer samples were used to describe prey availability in this study; a sweep-net would not have worked well in the densely vegetated stands.

Sixty activity traps (30 in *Carex* and 30 in *Equisetum*, the two most important vegetation types in the lake complex) were operated for 2 days in the beginning of September in 1998. Five corer samples (15.2 cm² each; see Hakala 1971) were taken in the beginning of August in 1993 in each of the same vegetation types. Combining data from different years can be a bit problematic. However, unlike North American prairie pot-holes, lakes in northern Europe are usually permanent and between year variation in water level is relatively small; and so is the variation in duck pair numbers and invertebrate abundance (Pöysä 1989, Nummi & Pöysä 1993). Pöysä *et al.* (2000) studied invertebrate abundance in 12 lakes for three years, and they found that there was a high concordance in the rank of lakes among years.

This indicates that at least invertebrate numbers are more stable here than in the prairies where water levels change dramatically and where ponds may even dry out (see e.g. Eisenlohr 1969, Pospisala *et al.* 1974). The averages of the prey size distributions given by the two methods were used in our analyses. Prey size distributions were calculated according to Nudds and Bowlby (1984).

When describing the overall invertebrate abundance of the lake complex studied, we used the invertebrate catch of 12 two-day activity trappings in May 1993. Food abundance was indexed by using the average catch per trap multiplied by the number of each prey taxon according to its average size. Prey were assigned to four size classes (0–2.5 mm 2.6–7.5 mm; 7.6–12.5 mm and > 12.5 mm) according to Nudds and Bowlby (1984), with small modifications (see Elmberg *et al.* 1993). This index is comparable with indices based on trappings done in 60 lakes around Fennoscandia in May 1990 or 1991 using exactly the same methods (Elmberg *et al.* 1993, Nummi *et al.* 1995). As compared with these 60 lakes, the prey abundance index (1468) of our lake complex studied here ranged very high. In 59 lakes of the previous study, the indices were lower (range 8–1251), in one outlier lake clearly higher (5284). Likewise, the density of dabbling duck pairs in spring was high. The mean dabbling duck density in lake Lapinjärvi in 1992–1997 was: 7.4 pairs km⁻¹ shoreline (V.-M. Väänänen, unpubl.); in the 60 Nordic lakes mentioned above, the mean dabbling duck density was 2.4 pairs km⁻¹ (range 0–15) (Elmberg *et al.* 1993), and only five lakes had more dense *Anas* populations than did our lake complex.

Results

Based on prey size distribution, the diets of all ducks differed from the environment (Figs. 1, 2 and Table 1: $P < 0.001$ in all cases [$G = 10.8$] except in the Garganey: $P < 0.05$, $G = 3.8$, d.f. = 1), although the differences were not very large (compare Nudds & Bowlby 1984). All species generally ate relatively large-sized invertebrates from size classes three and four (mainly isopods and gastropods) (Figs. 1, 2 and Appendix). Only shoveler and teal used invertebrates from size

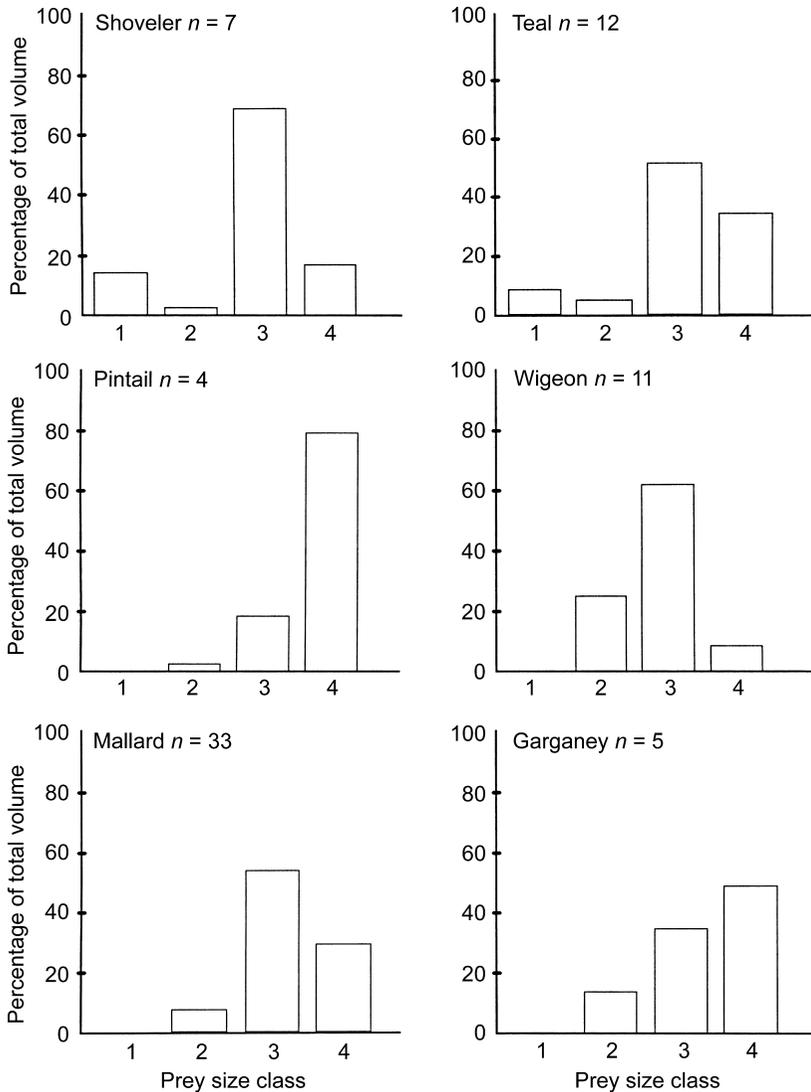


Fig. 1. Proportion of food available (volume) in different size classes in diets of dabbling ducks.

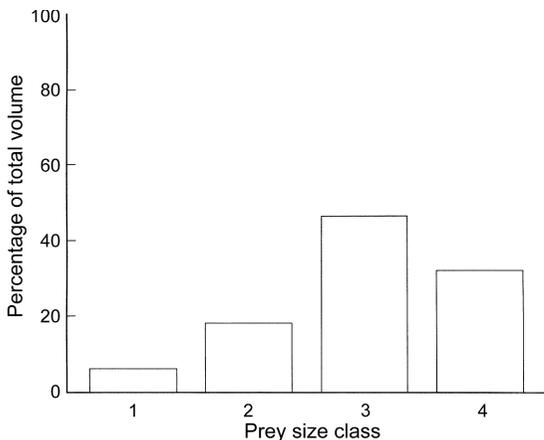


Fig. 2. Proportion of food available (volume) in different size classes in the environment.

class one.

Also, the size distributions of prey in the diet of different duck species varied ($G = 157.2$, d.f. = 10, $P < 0.001$). However, only 4 out of 15 of the G -values of the species pairs comparisons were significant (Table 2).

There was no relation between the lamellar density for different duck species and the mean prey length in their diet ($r_s = -0.374$, $P = 0.41$; excluding the wigeon who consumed very few invertebrates: $r_s = -0.700$, $P = 0.16$) (Fig. 3), although the species with finest lamellae (shoveler) also consumed the smallest prey.

There was not much segregation of food use

by the ducks along the vertical axis. Teal and wigeon differed from the other four species in the respect that they ate quite a lot of above-water invertebrates, such as aphids and adults of Ephemeroptera and Trichoptera (Table 3).

Discussion

In our study area, partitioning prey by size apparently was not the key factor enabling many dabbling duck species to occur together. Unlike Nudds and Bowlby (1984: number of species = 7), we did not find a significant correlation between the mean prey length in the diet of the ducks and the lamellar density of the ducks' bills ($n = 6$). Based on prey size selectivity, all the ducks of our study were on the "generalist" side of the generalist-specialist continuum of Nudds and Bowlby (1984). Also, based on prey size distribution, the diets of the sympatric ducks of our study seemed to differ statistically less often (4 out of 15) than the diets of the parapatric ducks in Nudds and Bowlby (1984; Table 3: 18 out of 21) (Fisher's exact test, $P = 0.04$).

Why might this be? Our study area clearly is at the luxuriant end of the prey abundance gradient of Nordic areas (see Study area and methods). So it may represent a situation where food resources are not limiting (Wiens 1993) and where resource overlap is high because of that (Wiens 1989, Nudds 1992). Food overlap linked with abundant resources has been found in shrub-steppe passerines (Rotenberry 1980), riparian insectivores (Rosenberg *et al.* 1982) and Galapagos ground finches (Schluter 1982a). In our study, the G -values for teal and mallard — comparing the diet and the environment — were

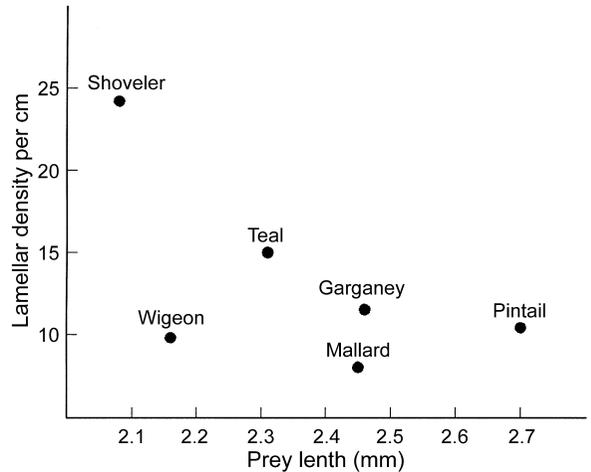


Fig. 3. The relationship between prey size (mean of log transformed prey size distributions) and mean lamellar density for six dabbling duck species. Lamellar density values from Nudds *et al.* 1994.

Table 1. Prey size selectivity by six species of dabbling ducks as indexed by the degree of departure of prey size distributions of diets compared with that in the environment. Values from the study of Nudds and Bolby (1984) are shown for comparison.

Species	G-values	
	Our study (samples sympatric)	Nudds & Bowlby (samples parapatric)
Garganey	6.6	46.1*
Teal	11.3	334.1
Mallard	11.4	95.7
Wigeon	17.2	219.9
Shoveler	35.8	289.8
Pintail	58.6	167.9

* Blue-winged teal *Anas discors*

Table 2. Matrix of pairwise species' differences in prey size distributions. Values of G from simultaneous test procedure are shown for all species pairs.

	Mallard	Pintail	Teal	Garganey	Shoveler
Pintail	44.0*				
Teal	1.4	44.2*			
Garganey	8.3	28.2	4.1		
Shoveler	9.5	88.9*	14.3	23.7	
Wigeon	29.0	121.3*	26.8	40.6	5.8

* Species pair differ at $P < 0.05$ ($G = 41.3$, d.f. = 28)

lower (reflecting a more generalistic way of foraging) than in the study conducted by Nummi (1993) in less invertebrate-rich lakes. This points to the possibility that food overlap was high because of luxuriant resources. It should be noted, however, that it is typical that we find the most abundant invertebrates in the very lakes where many dabbling ducks occur together — at least in northern Europe (Pöysä 1984, Elmberg *et al.* 1993). In Finland, for example, the shoveler and garganey breed only in food-rich lakes. In such lakes, invertebrates also are larger: in the 60 lakes mentioned before (*see* Study area and methods), the mean size of invertebrates correlated positively with invertebrate abundance (Nummi *et al.* 1995). All this suggests that the food availability and use patterns reported here may not be very exceptional.

Pöysä *et al.* (1994) found that deviation between observed and expected body length spacings according to null models tended to be greater in lakes with low food abundance than in lakes with high food abundance. The ducks of our eutrophic study area seemed not to partition the prey to a great extent on the vertical axis either, though we did not study feeding depths of the species. Teal and wigeon differed somewhat from the other four species: the relatively high use of above-water invertebrates by them reinforces the pattern shown in Jacobsen (1991) and Nummi (1993). The diets of our study were not very suitable in the consideration of the use of prey by different ducks along the vertical axis, because a large fraction of animal prey consisted of gastropods. In the luxuriant submerged vegetation, gastropods apparently are found all over the water column which confounds the prey use pattern along the vertical axis.

There evidently is much variation in abun-

dance patterns of certain invertebrates in different wetlands. In ours, isopods were especially numerous, and most likely also the gastropods. Gastropods most likely were somewhat underrepresented in our availability samples in spite of the use of the two different sampling methods. Wiens (1989) pointed out that, during resource scarcity, the relative abundance of only some foods may lead to convergence among species on these more common resources. The high number of certain invertebrates in our study seemed to coincide with a general resource abundance and, likewise, promoted relatively high overlap in food use between the different dabbling duck species. Schluter (1982b) has stated that animals probably do not even need to forage optimally when food is abundant.

Our study did not reveal much signs of partitioning prey by size among ducks. However, it is a typical “one shot” study (*sensu* Rotenberry 1980), covering only one part of the birds life cycle. For example, dabbling ducks assemblages may differ during winter from the ones found in summer. And, again, winter distribution patterns of dabbling ducks seem to differ between Europe and the American continent (Cramp & Simmons 1977). More studies, especially in the wintering grounds of Eurasia, are needed (*see* DuBowy 1988) in order to complement the knowledge of the organization of duck communities.

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Table 3. Percentage of animal foods of ducks divided into three classes according to their usual position in aquatic habitats.

	Wigeon (<i>n</i> = 11)	Teal (<i>n</i> = 12)	Mallard (<i>n</i> = 33)	Pintail (<i>n</i> = 4)	Shoveler (<i>n</i> = 7)	Garganey (<i>n</i> = 5)
Percentage of animals living over the water surface	23.6	27.7	0.8	–	5.3	0.5
Percentage of nektonic animals	–	0.7	1.2	–	1.4	–
Percentage of animals attached to underwater substrate	73.4	72.1	98.0	100.0	93.3	99.5

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Appendix. Proportion (%) of different prey of ducks in study area (+ = < 0.1%).

Prey	Wigeon n = 24	Teal n = 16	Mallard n = 36	Pintail n = 6	Shoveler n = 7	Garganey n = 5
Oligochaeta	—	—	+	0.1	—	—
Hirudinae	—	5.9	0.1	0.2	—	—
Cladocera	—	—	—	—	1.4	—
Copepoda	—	—	—	—	+	—
Isopoda	0.7	20.7	9.9	6.0	76.9	15.5
Aranea	—	0.2	+	—	—	—
Ephemeroptera a.	+	—	—	—	—	—
Ephemeroptera l.	—	—	+	—	—	—
Anisoptera l.	—	—	—	0.3	—	0.5
Zygoptera l.	—	—	0.3	—	0.1	—
Hemiptera	0.1	0.3	+	—	1.1	0.5
Trichoptera a.	—	0.6	—	—	4.0	—
Trichoptera l.	—	0.6	0.9	—	—	—
Coleoptera a.	0.1	+	—	—	—	—
Coleoptera l.	—	0.6	+	—	0.6	—
Dytiscidae a.	—	0.5	0.1	—	—	—
Dytiscidae l.	—	0.5	0.1	—	—	0.5
Diptera l.	—	—	0.1	—	—	—
Tipulidae l.	—	6.3	+	—	—	—
Chironomidae l.	0.3	3.4	0.1	0.1	1.1	24.3
Stratomyidae a.	0.1	—	—	—	—	—
Stratomyidae l.	—	13.2	0.1	—	—	—
Gastropoda	—	0.3	3.2	42.7	10.8	58.3
Valvatidae	—	—	0.6	0.1	—	—
Aphididea	—	19.0	—	—	—	—
Miscellaneous	0.2	0.6	+	—	1.1	0.1
Total animals (%)	1.5	72.7	15.8	49.4	97.1	99.7
Total plants (%)	98.5	27.3	84.2	50.6	2.9	0.3