

Occurrence and density of mallard and green-winged teal in relation to prey size distribution and food abundance

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We studied patterns of prey size and abundance among 60 lakes that differed with respect to occupancy by mallards (*Anas platyrhynchos*) and teal (*A. crecca crecca*). Size distributions of prey in lakes with and without mallards did not differ in the way they deviated from the prey size distribution found in the average diet of the species; the same was true also for teal. However, in lakes with abundant food, average teal diet differed more from what was found in the environment than in lakes with less prey; in the mallard there were no differences in this respect. The densities of mallard and teal correlated positively rather than negatively with each other irrespective of food abundance, suggesting that interspecific competition, at least in ecological time, between the species may not be important in determining their abundance and distribution.

1. Introduction

The distribution of organisms is often related to resource abundance and quality (e.g. Pulliam & Dunning 1987, Wiens 1989a). Because food is a potentially limiting resource, differential food use has been considered especially important for species coexistence (Schoener 1986, Wiens 1989a,b; but see Newton 1980). The importance of food partitioning by size has been stressed in many previous studies (e.g. Brown & Liebermann 1973,

Mares & Williams 1977, Thompson & Lawton 1983, Jaksić et al. 1993), although in some cases differences in prey size selection between species has not been found (e.g. Rotenberry 1980).

Among dabbling ducks (*Anas* spp.), clear prey size differences have been reported between species (Nudds & Bowlby 1984), and between mallards and teal collected at the same periods in the same area (Nummi 1993). Perhaps because of the omnivorous habits of many dabbling ducks, studies of diet differences based on prey taxa revealed only

few differences in food use except among the most specialized species (e.g. Swanson et al. 1979).

In this paper, we report on the occurrence and coexistence of mallard and green-winged teal (hereafter teal) in relation to both the amount of food and the prey size distribution available in lakes. Few food use studies document the size distribution of available prey (but see Gibb & Betts 1963, Smith et al. 1978, Thompson and Lawton 1983). We were able to compare the prey size distribution available with the prey size distribution in the diet of birds collected earlier from the same geographic area (Nummi 1993).

Mallard and teal were chosen for this study because of the relevant diet data available (Nummi 1993), and because they are the most common dabbling ducks in the study area (Danell & Sjöberg 1979, Pöysä 1984, Nummi & Pöysä 1995). Mallard and teal are the largest and smallest species of dabbling ducks. The density of lamellae in the feeding apparatus of their bill differ clearly (Pöysä 1983, Nudds et al. 1994), and correlate with differences in the size distribution of prey in diet (Nudds & Bowlby 1984, Nummi 1993). They also often are the only representatives of the dabbling duck guild present when food abundance is low (Pöysä et al. 1994).

Nudds and Bowlby (1984) suggested that dabbling ducks partition food resources according to prey size and Nudds et al. (1994) concluded that bill lamellar density allows different species of dabbling ducks to segregate among microhabitats according to size-based prey availability. We examined whether prey size and abundance in lakes influences coexistence of mallards and teal. Specifically, we asked (i) whether the occurrence, density, and coexistence of mallard and teal was related to abundance and/or size distribution of prey; and (ii) whether the densities of mallard and teal were negatively correlated, especially at the lower end of food abundance gradient.

2. Study area and methods

The study was conducted in 60 lakes in six regions between 56° and 67°N in Finland and Sweden in 1990 and 1991 (for a map, see Elmberg et al. 1993). The six regions represented a gradient from broad-leaved deciduous forest (South Sweden) to northern coniferous forest (North Finland). Of the study lakes, none were ephemeral, although some became

more shallow in late summer. Based on shoreline vegetation, ten lakes were selected in each region to represent the local gradient from barren to well-vegetated lakes (see Elmberg et al. 1993).

2.1. Duck counts

Ducks were censused in April and May using the waterfowl point count method (see Koskimies & Väisänen 1991). Two census periods were selected to detect both early and late breeding ducks (but see Elmberg et al. 1993). Two point counts were made in each period. Average numbers of the two counts then were used to calculate pair density per kilometer of shoreline. "Mallard lakes" are those which had mallards but which also may have contained other dabbling ducks (also teals); "teal lakes" likewise had teal and possibly other ducks (also mallards). "Only-mallard lakes" had only mallards (in one lake also wigeon), but, because there were practically no lakes with only teal, "only-teal lakes" could not be considered. "Non-mallard lakes" did not have mallard and "non-teal lakes" did not have teal. "Environment" refers to all the 60 lakes.

2.2. Invertebrate sampling

Invertebrates were sampled during the two duck census periods with activity traps (Murkin et al. 1983). The traps were made from 1-litre glass jars and funnels with an external diameter of 100 mm and an internal diameter of 23 mm. Traps were placed on the bottom for 48 hrs (Elmberg et al. 1992). Ten activity traps were placed in each lake per sampling period, except in Finland where four traps were used in the first sampling period. Traps were set parallel to the shore, 1 m from the water's edge or at the outer edge of emergent vegetation, where the water depth ranged between 25–75 cm (details in Elmberg et al. 1993).

Food abundance for each lake was indexed by using the average catch per trap of the pooled data, multiplied by the number of each prey taxon by 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, Table 2) with small modifications (see Elmberg et al. 1993). The multiplied figures also were used to obtain a proportional size-class distribution of prey in each lake. These size-class distributions then were compared to those found in the average diets of mallard and teal (obtained from Nummi 1993) in which birds' diets are expressed in energy distributions. Volumetric and energy-based distributions did not differ (G -value for mallard = 0.743; teal = 0.583; $P > 0.50$ for both).

Because resource levels may strongly affect patterns of food use and the potential for competition (Wiens 1989b, 1993), we studied whether mallard and teal densities responded differently to each other in different parts of the prey abundance gradient. This was done by dividing the 60

lakes in one group of high (30) and one of low (30) prey abundance. We predicted that bird densities would respond to each other in particular in the low end of prey abundance. To examine whether it is the smaller or larger species that is present in the most barren habitats, we checked lake occupancy by the birds in six lakes of the very low end of the resource abundance gradient. To study whether the kinds of prey available varied with resource abundance, we examined the correlation between each of mean prey size and diversity of prey size classes (Simpson's index [Begon et al. 1990]) with prey abundance.

2.3. Statistical procedures

The prey size distribution in the average diet of the mallard and teal, respectively, was compared with the prey size distribution in each lake using *G*-tests (see Nudds & Bowlby 1984). The *G*-test was not used as a test of statistical significance, but rather as an index of relative difference between prey size distribution in average duck diet and in a particular lake, hereafter the "deviation index" (*DI*): the smaller the index the more tightly the average prey size distribution in duck diet fits that found in the lake. The deviation index was then compared between species or with food abundance by means of Spearman rank correlation and Mann-Whitney *U*-test.

3. Results

The sizes of prey in the average diet of mallards differed more from the environment than did sizes of prey in the diet of teal (Tables 1 and 2). There were similar differences between mallard *DI*'s of mallard lakes and teal *DI*'s of teal lakes (Table 2).

The *DI*'s of mallard lakes did not differ from those of non-mallard lakes, nor did the *DI*'s of teal-

lakes with teal differ from those of non-teal lakes (Table 2). The *DI*'s of mallard did not correlate with resource levels ($r_s = 0.04$, $P > 0.05$) but those of teal did ($r_s = 0.53$, $P < 0.001$). When prey is abundant, the size distribution of prey in the average teal diet deviates more from that available in the environment.

There was no correlation between resource levels and the degree to which the size distribution of prey in mallard and teal diets (according to Nummi 1993) differed from that available in the environment: mallard deviation index (*DI*) vs. food abundance $r_s = -0.074$, $P > 0.05$; teal *DI* vs. food abundance $r_s = -0.098$, $P > 0.05$. Mean prey size correlated with prey abundance ($r_s = 0.529$, $P < 0.0001$, Fig. 1), whereas prey size diversity did not ($r_s = 0.047$, $P > 0.05$). In general, food of size class three was most abundant (Table 1).

Mallard density increased with prey abundance and teal density tended to do so, too (Table 3). The densities of the two species also correlated positively with each other, regardless of overall resource abundance. Out of the six lakes at the low end of the resource abundance gradient, mallards occupied all with an average density of 0.69 pairs per kilometer shoreline; teals were present in only three lakes in which their average density was 0.40 pairs/km.

The amount of food did not differ between lakes where both mallard and teal were present and lakes with only mallards ($Z = -0.72$, $P > 0.05$).

Table 2. Comparisons of deviation indices (*DI*) for mallard and for teal. Mann-Whitney *U*-test. (Mean *DI*-values and sample sizes in parentheses).

	<i>Z</i>	<i>P</i>
Mallard <i>DI</i> (89.6) vs. teal <i>DI</i> (62.9) (all 60 lakes)	-3.93	0.000
Mallard <i>DI</i> in mallard lakes (101.8; 47) vs. teal <i>DI</i> in teal lakes (66.5; 29)	-2.71	0.007
Mallard <i>DI</i> in mallard lakes (101.8; 47) vs. mallard <i>DI</i> in non-mallard lakes (92.5; 13)	-0.32	0.747
Teal <i>DI</i> in teal lakes (66.5; 29) vs. teal <i>DI</i> in non-teal lakes (59.6; 31)	-1.05	0.294

Table 1. Average proportion of food available in different size classes in 60 lakes and in the average diets of mallard and teal (diets from Nummi 1993). Size classes: 1: 0–2.5 mm; 2: 2.6–7.5 mm; 3: 7.6–12.5 mm; 4: 12.6–20 mm.

Size class	1	2	3	4
	%	%	%	%
The environment, average	13	5	44	8
Mallard diet	1	46	11	42
Teal diet	24	31	21	22

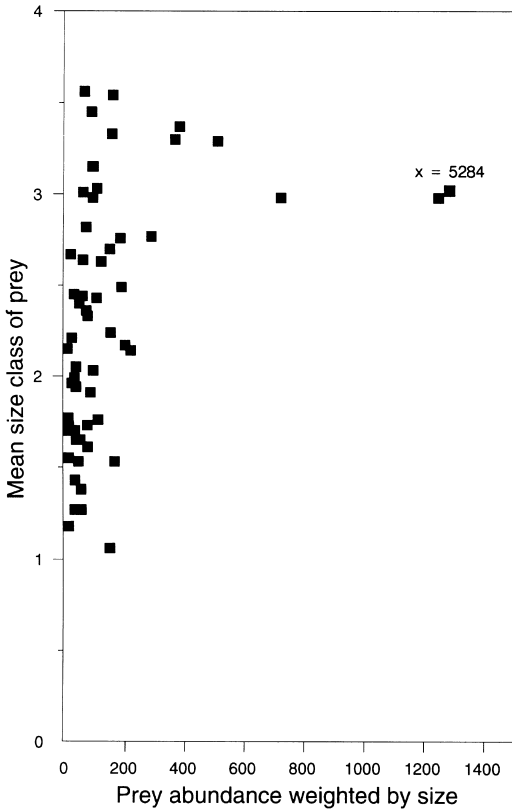


Fig. 1. Mean size class of prey in relation to prey abundance in 60 lakes in Sweden and Finland ($r_s = 0.529$, $P < 0.0001$, $N = 60$). For the one outlier point its x-axis value is given.

Table 3. Correlation of mallard and teal densities with food abundance and with each other; duck densities are compared with each other separately in lakes of low and high prey abundance. Spearman rank correlations.

	r_s	Probability
Mallard density vs. food abundance (60)	0.28	0.031
Teal density vs. food abundance (60)	0.21	0.107
Mallard vs. teal density, all lakes (60)	0.56	0.000
Mallard vs. teal density, low prey abundance (30)	0.60	0.001
Mallard vs. teal density, high prey abundance (30)	0.49	0.008

However, they both had more food than lakes without either of the two species ($P < 0.05$ in both cases). The combined mallard-teal density was higher in lakes with mallard and teal than in lakes with only mallards ($Z = -4.70$, $P = 0.000$); also the density of mallards was higher in lakes with mallard and teal ($Z = -2.97$, $P > 0.005$).

4. Discussion

In the Fennoscandian lakes we studied, there was no systematic change in prey size diversity along the prey abundance gradient. However, in general, a greater proportion of prey was available in the larger size classes. The distribution of ducks among lakes was not correlated with the size distribution of prey in lakes, but with the amount of food. Hespeneide (1971) concluded that "the average prey size of prey taken by insectivorous birds is always larger than that available to them". The pattern of prey selected was not clearcut in this study. The average diet of the teal even seemed to contain more prey from smaller size classes that was available in the 60 lakes of the present study (see also Nummi 1993).

It has been hypothesized that an overall decrease of resources should lead to reduced overlap in use of prey by potential competitors (Wiens 1977, 1989b, DuBowy 1988, Nudds 1992, but see Wiens 1993). Sometimes species of a guild may maintain species-specific means of their prey regardless of shifts in prey availability (Jaksic et al. 1993). Pulliam (1985), however, found that different species of opportunistic sparrows are likely to have broadly overlapping diets whenever seeds are scarce enough for the consumption of seeds by one species to have much impact on the availability of seeds to another species. The wide size-spectrum and overlap in mallard and teal diets have also been documented (Nummi 1993).

In this study, we did not investigate shifts in the use of the prey size gradient *per se* but the occurrence and coexistence of mallard and teal indicated that prey size gradient was of minor importance. However, more effort is needed on duck diets and on availability of prey in different parts of the aquatic ecosystem in order to make the picture of prey partitioning by size more clear.

Distribution of ducks among lakes correlated with amount of food. According to Pulliam (1983), there should be a section along the food resource gradient where only the energy demands of the smallest species of a guild are met (see also Hanski & Kaikusalo 1989). The wide lamellar spacing of the large mallard (Nudds & Bowlby 1984, Nudds et al. 1994, Mott 1994) should make the collection of smallest prey much less profitable than it is for the small teal with its dense lamellar spacing.

However, in this study, mallards occupied lakes at least at the same point in the resource abundance gradient, if not lakes with fewer resources than teal. It may be that larger benthic animals, which are consumed especially by mallards (Perret 1962, Nummi 1993), will be abundant enough to support mallards at the low end of the abundance gradient; and that only in lakes where resources are more abundant will the smaller, nektonic prey support teal. Nevertheless, teal may be present without mallards in small habitat patches with a very narrow zone for benthic foraging (Nummi & Pöysä 1995). Similarly, Brown and Liebermann (1973) found that the largest rodent species of their study inhabited all kinds of habitats. They speculated that this may be because the relative abundance of large seeds was high and because food resources were scarce and clumped (see also Hanski 1985).

Possible competition along prey size and resource abundance gradients studied here did not seem to strongly affect the distribution of teal and mallard. Schluter (1982) found that interspecific competition was not as important a factor as variation in food supply in affecting ground finch distributions. It is noteworthy that also at the lower end of the resource gradient, where resource limitation is most likely to occur (Wiens 1989b), the density of mallard and teal correlated positively. However, the low numbers of teal in lakes of relatively low food abundance and mallard presence could be explained at least partly by interference competition (Pulliam 1985). Pulliam (1985) stated that in situations of rather low food abundance the largest species would exclude all others, and, when resources are slightly more abundant, should first tolerate the smallest species of the guild.

In evolutionary time competition may have affected the food niches of mallard and teal in a way which promotes their coexistence even in low food situations. The size of mallard and teal differs clearly

and the lamellar densities of their bills are very different (Pöysä 1983, Nudds et al. 1994). However, this study showed little evidence for present day competition between the two species.

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