Comparative feeding behaviour and niche organization in a Mediterranean duck community

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Abstract: Feeding behaviour of the Marbled Teal, *Marmaronetta angustirostris*, Mallard, *Anas platyrhynchos*, Garganey, *Anas querquedula*, and Ferruginous Duck, *Aythya nyroca*, in the Göksu Delta, Turkey, was compared from 10 July to 6 August 1995. Almost all individuals observed were postbreeding adults and juveniles. Marbled Teal fed closest to the surface (mean depth within the water column 8.4 cm), chiefly by bill dipping (66%) and gleaning (14%). Garganey fed at a mean depth of 9.1 cm, mainly by bill dipping (57%) and neck dipping (35%). Mallards fed at greater depths (mean 31.8 cm), mainly by upending (tipping 46%) and neck dipping (41%). Ferruginous Ducks fed at the greatest depths (mean 38.4 cm), chiefly by diving (76%). Marbled Teal moved most frequently between feeding events and Mallards moved least frequently. As in previous studies of dabbling ducks, the largest species (Mallard) upended more and fed deeper in the water column. However, Mallards used shallower microhabitats than smaller dabbling ducks. Dabbling and diving duck guilds were not discernible in either horizontal (feeding habitat) or vertical (feeding behaviour) niche dimensions, and the Mallard and Ferruginous Duck were related in both dimensions. Niche overlaps between species pairs along the two dimensions were negatively correlated ($r = -0.71$, $P = 0.12$), supporting niche complementarity.

Résumé : Le comportement alimentaire a été comparé chez quatre espèces de canards, la Marmaronette marbrée, *Marmaronetta angustirostris*, le Canard colvert, *Anas platyrhynchos*, la Sarcelle d'été, *Anas querquedula*, et le Fuligule nyroca, *Aythya nyroca*, dans le delta de Göksu, Turquie, du 10 juillet au 6 août 1995. La plupart des canards observés étaient des adultes post-reproducteurs et des juvéniles. Ce sont les Marmaronettes marbrées qui se nourrissent le plus en surface (profondeur moyenne de 8,4 cm dans la colonne d'eau), surtout par immersion du bec (66%) et par grappillage (14%). Les Sarcelles d'été se nourrissent à une profondeur moyenne de 9,1 cm, surtout par immersion du bec (57%) et immersion du cou (35%). Les Canards colverts se nourrissent plus profondément (31,8 cm en moyenne), surtout par basculement (46%) et par immersion du cou (41%). Les Fuligules nyroca sont les canards qui se nourrissent aux plus grandes profondeurs (38,4 cm en moyenne), surtout par plongée (76%). Ce sont les Marmaronettes marbrées qui se déplacent le plus souvent entre les sessions d'alimentation et les Canards colverts qui se déplacent le moins souvent. Comme l'ont démontré d'autres études sur les canards barboteurs, la plus grande espèce (le Canard colvert) a plus recours au basculement et se nourrit plus profondément dans la colonne d'eau. Cependant, le Canard colvert utilise les microhabitats d'eau moins profonde que les canards barboteurs plus petits. La guilde des canards barboteurs et celle des canards plongeurs ne diffèrent pas d'après les dimensions horizontales (habitat alimentaire) ou verticales (comportement alimentaire) de leurs niches respectives et les Canards colverts et les Fuligules nyroca sont semblables dans les deux dimensions. Les parties superposées des niches de paires d'espèces le long des deux dimensions sont en corrélation négative ($r = -0{,}71$, $P = 0{,}12$), ce qui appuie l'hypothèse de la complémentarité des niches.

[Traduit par la Rédaction]

Introduction

Various studies of habitat use by duck communities have shown niche separation between species in horizontal dimensions such as wetland size, vegetation characteristics, and water chemistry (Bengston 1971; Weller 1975; White and James 1978; Amat 1982; Toft et al. 1982; Anderson and Ohmart 1988; Monda and Ratti 1988; Bergan and Smith 1989; Nummi and Pöysä 1993; Nudds et al. 1994). Some studies have addressed vertical partitioning in foraging methods and in the depths in the water column at which feeding occurs (Danell and Sjöberg 1982; Thomas 1980, 1982). However, few studies have addressed these issues simultaneously to identify the relationship between horizontal and vertical partitioning in duck communities. Amat (1984*a*) showed that the Red-crested Pochard, *Netta rufina,* and Common Pochard, *Aythya ferina*, used different habitats but shared feeding methods in winter, then shared the same habitat but used distinct feeding methods in spring. Pöysä (1983*a*, 1983*b*) found that partitioning of feeding methods was more important in dabbling ducks, while partitioning of feeding habitats was more important in diving ducks. Pöysä (1987) found a nonsignificant negative correlation between niche breadth in the horizontal (feeding sites) and vertical (feeding method) resource axes for dabbling ducks and Amat (1984*b*) obtained a similar result for diving ducks. These findings support niche complementarity (Schoener 1974).

In this study I compare the feeding behaviour in late summer of four species in the Göksu Delta, Turkey: the Marbled Teal, *Marmaronetta angustirostris*, the Mallard, *Anas platyrhynchos*, the Garganey, *Anas querquedula*, and the Ferruginous

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Duck, *Aythya nyroca*. Strong partitioning in habitat use occurs between species in this community (Green 1996[1], Green 1998). Here I consider the relationship between horizontal partitioning in feeding habitat and vertical partitioning in feeding behaviour. I ask how feeding depth is related to the depth of microhabitats exploited by each species. I consider whether the dabbling and diving ducks form separate guilds in this community and I test for niche complementarity. I also consider the relationship between feeding behaviour and body size in dabbling ducks in the light of the results of previous studies suggesting that larger species feed lower in the water column (Pöysä 1983*a*; Nudds 1992).

The Marbled Teal and Ferruginous Duck are globally threatened species (Collar et al. 1994; Tucker and Heath 1994; Green 1996), and this is the most detailed study to date of their foraging ecology (but see Amat and Soriguer 1982; Navarro and Robledano 1995). The Garganey has been studied at breeding sites (Pöysä 1983*a*, 1983*b*, 1986), but as far as I am aware, this is the first ecological study of postbreeding migration. The Marbled Teal was long considered a typical surface-feeding duck, but is now considered the living member of the Aythyini (pochards) that bears the closest resemblance to the ancestor of this tribe (Johnsgard 1961; Livezey 1996). In this study I consider the Marbled Teal to be a "dabbling duck," using the term in the ecological rather than the taxonomic sense.

Study area

The Göksu Delta is located on the Turkish Mediterranean coast (see DHKD 1992; Green 1996[1]; for a detailed description see Green 1998). It is a Ramsar site (Frazier 1996), a Specially Protected Area, and an Important Bird Area (Magnin and Yarar 1997), and supports internationally important breeding populations of Marbled Teal (ca. 50 pairs) and Ferruginous Ducks (ca. 30 pairs), as well as about 50 pairs of Mallards. Garganeys use the delta on postbreeding passage, beginning to arrive in early July, with numbers peaking at 3000–5000 in late August (Green 1996[1]). Breeding and postbreeding ducks are highly concentrated at Lake Akgöl, a permanent, well-vegetated, freshwater to brackish eutrophic lake (1400 ha) with extensive beds of *Phragmites australis*, *Typha* sp., *Scirpus* (= *Schoenoplectus*) *litoralis*, and *Potamogeton pectinatus*.

This study was conducted when Mallards had completed breeding and large numbers of postbreeders from other areas were present. Marbled Teal and Ferruginous Ducks were at the end of their breeding season, and some broods had not yet fledged when this study began. However, ducklings were excluded from this study and almost all individuals included were postbreeding adults or juveniles.

Methods

From 10 July to 6 August 1995 inclusive, Akgöl and other wetlands in the delta (see Green 1996[1]; for details see Green 1998) were systematically surveyed three times for Anatidae. All areas of Lake Akgöl accessible by canoe were surveyed over several days. Fieldwork was conducted from first light (06:45 local time) and was usually completed by 14:00. Three complete surveys of Lake Akgöl were conducted over the periods 18–23 July, 24–28 July, and 30 July – 5 August, dates inclusive.

Ducks were observed with a telescope during a total of 150 h of fieldwork. All male Mallards and Garganeys were in eclipse plumage. Breeding and eclipse plumages could not consistently be distinguished for the Marbled Teal or Ferruginous Duck, although some adults of both species were clearly molting. Some flightless Garganeys were observed. Owing to the distances and light conditions in which observations were made, it was rarely possible to distinguish the sexes, or adults from juveniles, so all observations were pooled for each species.

The behaviour of each duck feeding at the time of initial observation was recorded as one of the following: dive; upend (tipping); neck dip (part or all of neck submerged); head dip (eye submerged); bill dip (part or all of the bill submerged); glean (bill held in the plane of the water surface with only the lower mandible submerged, straining items from the water surface). Feeding birds were described as mobile or static, mobile birds being those moving during more than 50% of interdive intervals or intervals between other foraging events (upends, dips, etc).

For each individual Mallard, Marbled Teal, and Ferruginous Duck seen feeding, the following details of its position at the time of initial observation were recorded: distance to the nearest emergent vegetation (estimated visually in metres); species of emergent vegetation; presence or absence of submerged macrophytes at the surface layer. Suspected repeated observations of the same individual on the same day were discarded. Garganeys were observed in large flocks of up to several hundred, and the above data were recorded for a random sample of feeding individuals.

A dipstick was used to measure water depth at locations where Marbled Teal and Ferruginous Ducks were feeding. Although some species of Aythyini do not always feed on the bottom when diving (Tome and Wrubleski 1988), diving depth for feeding was assumed to be water depth, since observations of bill contents and behaviour upon surfacing, combined with grab and net sampling, suggested that all diving birds were feeding on benthic seeds or *Chara vulgaris*, which was confined to the bottom of the water column. Feeding depth for gleaning was considered to be 1 cm and for other feeding methods was estimated using morphological measurements from museum specimens (Appendix) following Pöysä (1983*a*): for upend this was 3/5 × body length + neck length; for neck dip it was neck length; for head dip it was skull length; and for bill dip it was bill length.

Niche organization for feeding birds was compared for the horizontal (habitat use) and vertical (feeding behaviour) axes. Percent niche overlap between resource categories (Krebs 1989) was used to calculate overlap for each species pair for the following habitat-use variables: nearest emergent vegetation type; distance to nearest emergent vegetation; presence or absence of *P. pectinatus* in the surface layer (Table 1). Since these three variables were not independent, mean niche overlap was calculated as an overall measure of horizontal partitioning (see Pöysä 1983*b*; Monda and Ratti 1988). Likewise, mean niche overlap for feeding behaviour was calculated using feeding method and depth data (see Figs. 1 and 2). Cluster analysis was used to produce dendrograms based on interspecific distances in the horizontal and vertical dimensions (UPGMA method; Krebs 1989).

Results

Feeding behaviour

Strong differences in feeding method were observed between duck species (Fig. 1). Marbled Teal fed mainly by mobile bill dipping and were the only species observed gleaning and the only dabbling duck observed diving. Dive times for juvenile Marbled Teal were recorded on 30 July, when they were diving to a depth of 49 cm (n = 17, range 2–7 s, 4.9 ± 1.5 s (mean ±

[1] A.J. Green. 1996. The summer ecology of the Marbled Teal *Marmaronetta angustirostris*, Ferruginous Duck *Aythya nyroca* and other ducks in the Göksu Delta, Turkey in 1995. Unpublished report, Estación Biológica de Doñana, Seville, Spain.

Table 1. Percentage of feeding duck observations by category among three habitat variables in Lake Akgöl.

	Mallard (n = 110)	Garganey (n = 70)	Marbled Teal (n = 24)	Ferruginous Duck (n = 41)
Nearest emergent vegetation				
Scirpus litoralis	38.2	33.9	70.8	45.0
Phragmites australis	26.4	8.1	25.0	35.0
Typha sp.	35.5	58.1	4.2	20.0
Distance to emergent vegetation (m)				
0	3.6	0	8.3	0
1	20.9	6.5	0	27.5
2–5	43.6	9.7	58.3	42.5
6–10	21.8	12.9	16.7	5.0
11–50	10.0	61.3	16.7	25.0
>50	0	9.7	0	0
P. pectinatus at surface?				
Yes	95.4	94.3	75.0	75.6
No	4.6	5.7	25.0	24.4

Table 2. Feeding-niche overlaps between duck species for horizontal (above the diagonal) and vertical (beneath the diagonal) resource axes.

	Mallard	Garganey	Marbled teal	Ferruginous Duck
Mallard	—	0.72	0.74	0.81
Garganey	0.28	—	0.55	0.63
Marbled Teal	0.14	0.67	—	0.79
Ferruginous Duck	0.29	0.22	0.30	—

Note: Horizontal overlaps are means of three dimensions (nearest emergent vegetation; distance to emergent vegetation; presence or absence of submerged vegetation). Vertical overlaps are means of two dimensions (feeding method; feeding depth).

SD)). Ferruginous Ducks fed mainly by diving, whilst Mallards fed chiefly by static upending (tipping) and neck dipping (Fig. 1). Garganeys fed largely by static bill and neck dipping (Fig. 1). Differences in feeding method among species were highly significant ($\chi^2 = 429$, 15 df, $P < 0.0001$), even when Ferruginous Ducks were excluded ($\chi^2 = 193$, 10 df, $P < 0.0001$).

As a result of the differences in feeding method, each species was feeding at different depths within the water column (Fig. 2). Marbled Teal were ingesting food at the shallowest depths (range 1–49 cm, 8.4 ± 12.1 cm), followed by Garganeys (range 4–18 cm, 9.1 ± 6.7 cm) and then Mallards (range 6–41 cm, 31.8 ± 10.3 cm). Ferruginous Ducks were feeding at the greatest depths of all (range 4–50 cm, 38.4 ± 17.6 cm). Differences in feeding depth among species were highly significant (Kruskal–Wallis test, $H = 190$, 3 df, $P < 0.0001$).

Whereas Marbled Teal and Garganeys in Lake Akgöl fed mainly in the top half of the water column, amongst beds of *P. pectinatus* that filled the surface layer (Table 1), Ferruginous Ducks fed mainly at the lake bottom. Mallard were intermediate, but most upending birds and many of the neck-dipping ones were probably feeding at the lake bottom (Green, see footnote 1; Green 1998). Lake depth at feeding sites used by Marbled Teal (n = 16, range 31–66 cm, 47.9 ± 10.3 cm) and Ferruginous Ducks (n = 9, range 30–51 cm, 46.3 ± 7.0 cm) within Lake Akgöl were very similar (two-tailed two-sample t test, $t = 0.44$, 22 df, $P = 0.66$). Maximum lake depth at the time of the study was 100 cm (Green, see footnote 1).

Marbled Teal moved more often between foraging events than the other species did (Fig. 1). Excluding unknowns, 92.0% of feeding Marbled Teal (n = 50), 45.5% of Ferruginous Ducks (n = 44), 16.0% of Garganeys (n = 81), and only 5.3% of Mallards (n = 113) were mobile. These differences among species were highly significant ($\chi^2 = 138$, 3 df, $P < 0.0001$), and remained similar when the analysis was confined to those behaviours (bill, head, and neck dipping) exhibited by all four species (90.5% of Marbled Teal (n = 42), 53.8% of Ferruginous Ducks (n = 13), 16.0% of Garganeys (n = 81), and 7.8% of Mallards (n = 64) were mobile; $\chi^2 = 96$, 3 df, $P < 0.0001$).

Niche segregation

There was a nonsignificant negative correlation between niche overlaps shown between species pairs along the vertical (feeding behaviour) and horizontal (feeding habitat) resource axes (Table 2; $r = -0.705$, $P = 0.12$). This correlation is strongly affected by the Marbled Teal – Garganey pair, which had the most similar vertical niches and the least similar horizontal niches (Table 2). Cluster analysis showed that along the vertical resource axis, the Marbled Teal and Garganey were very similar, whilst the Mallard and Ferruginous Duck were related to each other, but with much less similarity (Fig. 3*a*). Along the horizontal resource axis, the Mallard and Ferruginous Duck were again grouped together, but with much greater similarity (Fig. 3*b*). The Garganey was isolated from the other three species in horizontal niche space (Fig. 3*b*).

Discussion

Marked differences in feeding method were found between the

Fig. 1. Proportions of Mallards ($n = 134$) (*a*), Garganeys ($n = 81$) (*b*), Marbled Teal ($n = 58$) (*c*), and Ferruginous Ducks ($n = 62$) (*d*) using different feeding methods in the Göksu Delta. See Methods for a full description of feeding methods. Birds "not recorded" are those for which the distinction between "mobile" and "static" feeding was not made. Data exclude ducklings but include one adult Marbled Teal (bill dip) and one adult Ferruginous Duck (head dip) accompanying broods.

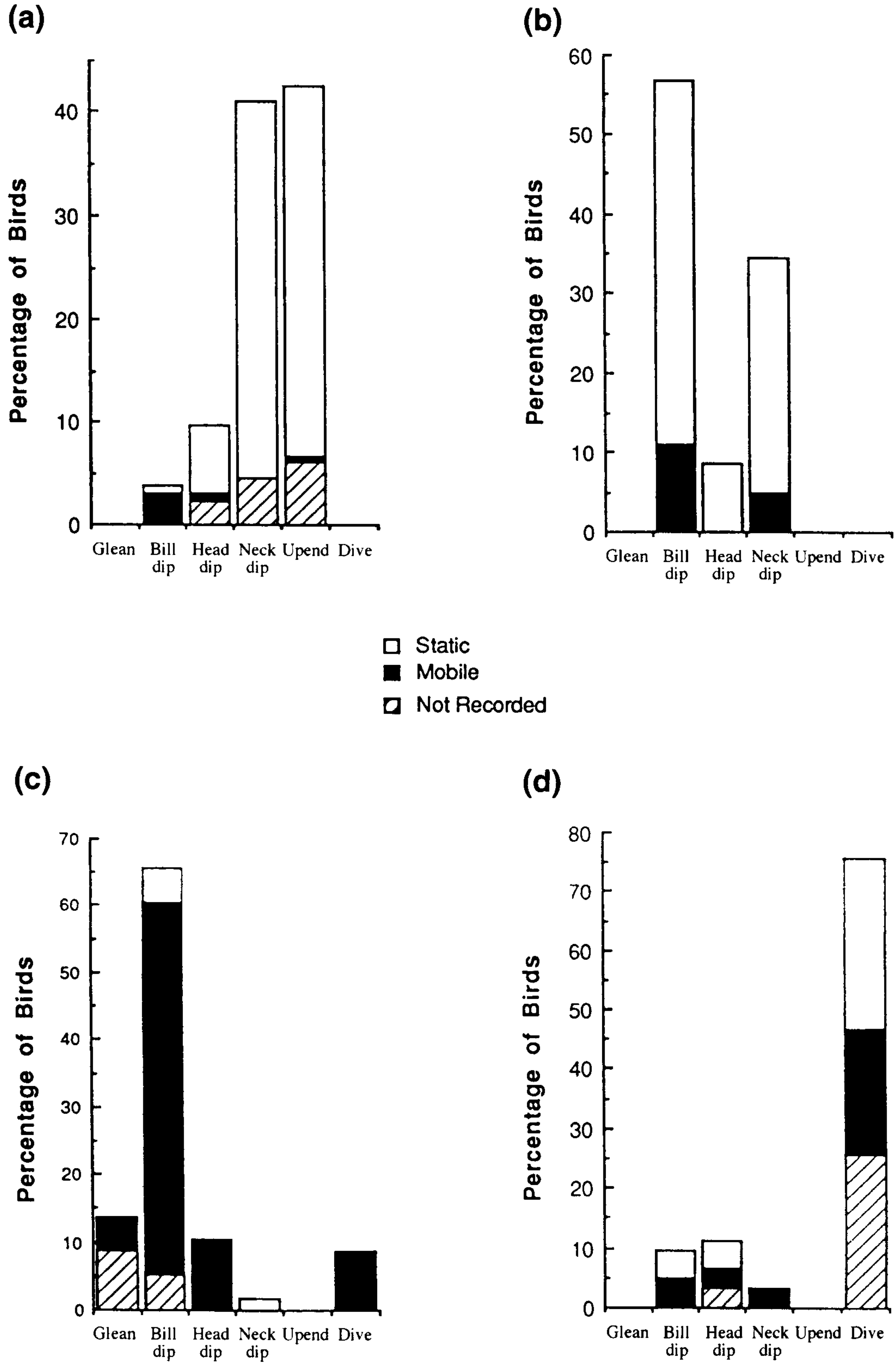
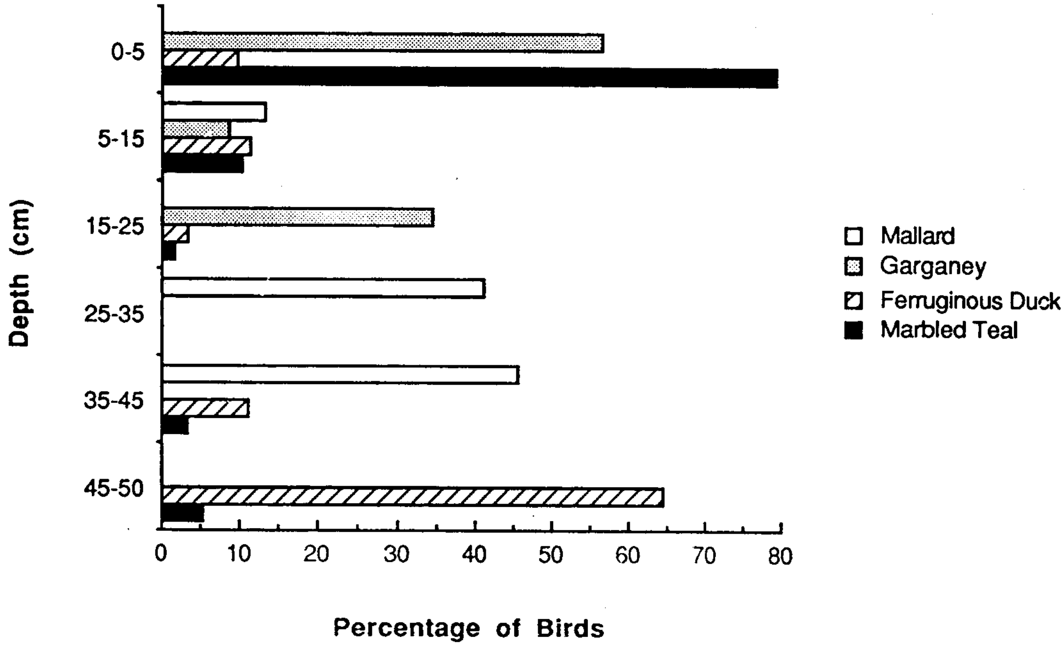


Fig. 2. Feeding depths used by duck species in the Göksu Delta. See Fig. 1 for sample sizes. These figures refer to the depth within the water column at which ingestion occurred, which was often much less then the total depth of the water column (see Methods).



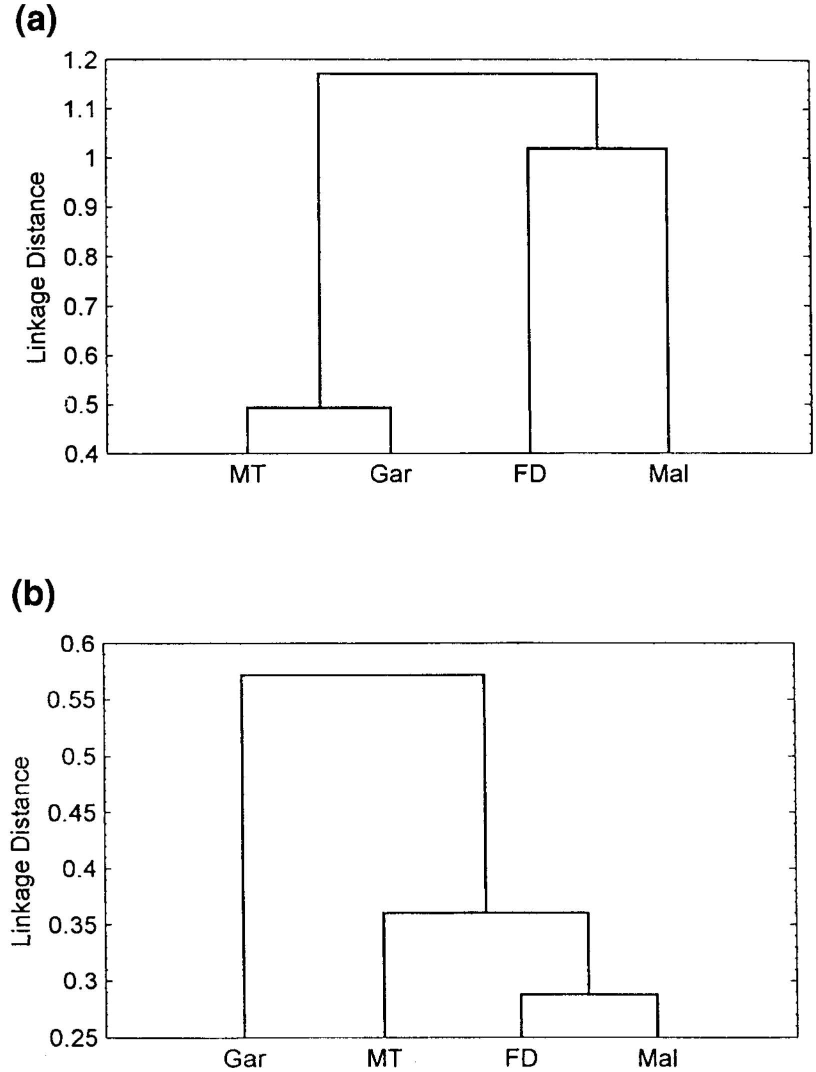
four duck species studied, resulting in clear vertical separation of feeding activity in the water column. This complements differences in habitat use and diet (Green, see footnote 1; Green 1998). Marbled Teal fed closest to the water surface, which confirms that this species is a dabbling duck in ecological terms, despite its taxonomic position in the Aythyini (Livezey 1996). Not surprisingly for an *Aythya* species, Ferruginous Ducks fed at the greatest depths, although their average feeding depth was only 21% more than that of Mallards. Indeed, Mallards showed greater overlap with Ferruginous Ducks in the depth ranges utilized (23% according to Fig. 2) than with the other two dabbling duck species (14% with the Marbled Teal and 9% with the Garganey). Similarly, the Marbled Teal and Garganey showed much more overlap with each other (67%) than with either of the other two species.

Amongst previous studies of dabbling ducks, larger species (e.g., Mallard, Northern Pintail, *Anas acuta*) fed lower in the water column than smaller species (e.g., Garganey and Green-winged Teal, *Anas crecca*), partly because they showed a greater tendency to upend (Danell and Sjöberg 1982; Thomas 1980, 1982; Pöysä 1983*a*, 1983*b*; Nudds 1992). The results of the present study, which included the previously unstudied, relatively small Marbled Teal, confirm this pattern. It therefore seems to be a fairly universal rule that larger dabbling ducks upend more, and Pöysä (1983*a*) proposed that this is because it is more energetically efficient for them to do so, since they can remain submerged longer. He proposed that smaller species are selected to feed mainly at the surface, partly because their lower energy requirements are easier to meet without upending. Alternatively, I propose that this upending rule may be explained by diminishing benefits of upending for smaller species, owing to the smaller increase in accessible depths (see Fig. 8 in Thomas 1982 and Fig. 1 in Pöysä 1983*a*).

The differences in feeding method observed in this study were connected with differences in food selection, although all four species fed mainly within dense beds of *P. pectinatus* (Table 1). Gleaning Marbled Teal were feeding on dense, floating concentrations of relatively small *S. litoralis* seeds, whilst those feeding in other ways were taking mainly insects. Mallards were feeding mainly on the basal parts of *P. pectinatus* and on charophytes (*Chara vulgaris*) (Green, see footnote 1). Garganeys were probably consuming mainly the upper parts of *P. pectinatus*, whereas Ferruginous Ducks were probably diving to feed on the seeds of *P. pectinatus*, *Potamogeton panormitanus*, and *S. litoralis* abundant in the benthos, and taking *P. pectinatus* seeds when feeding by other methods (Cramp and Simmons 1977; Green, see footnote 1; Kear and Wildfowl and Wetlands Trust 1998).

Owing to their physical advantage when feeding at greater depths, larger dabbling duck species may often exploit deeper habitats (e.g., Euliss and Harris 1987). However, Pöysä (1983*a*) found only a weak, nonsignificant positive correlation between neck length and the mean depth of feeding habitat, and White and James (1978) found that Mottled Ducks, *Anas fulvigula,* used shallower habitats than six smaller *Anas* species. In the Göksu Delta, there was a negative relationship between feeding depth and depth of the habitat used, since Mallards made most use of shallower parts of Lake Akgöl and Marbled Teal made most use of deeper parts (Green, see footnote 1; Green 1998). The results of the current study show that there was no difference in lake depth between areas selected for foraging by Marbled Teal and Ferruginous Ducks, in spite of the major difference in feeding depth. This was largely a consequence of the dense beds of *P. pectinatus* in the surface layer of relatively deep parts of the lake, providing plant and invertebrate food for ducks close to the water surface. In a lake where submerged vegetation was only available towards the bottom of the water column, Pöysä (1983*a*) found

Fig. 3. Dendrograms showing similarity (Euclidean distances) between duck species in feeding behaviour (vertical partitioning) (*a*) and feeding habitat (horizontal partitioning) (*b*) in the Göksu Delta. FD, Ferruginous Duck; Gar, Garganey; Mal, Mallard; MT, Marbled Teal.



that Mallards fed in deeper parts than Garganeys. Similarly, in sites in Spain where submerged vegetation was rare and ducks foraged in the sediments, Marbled Teal fed in shallower areas than larger ducks such as Mallards (A.J. Green, unpublished data).

Unfortunately, data collected in this study are too limited to reflect the variation in feeding behaviour shown by ducks in response to differences in season, sex, age, depth fluctuation, and even time of day (Danell and Sjöberg 1982; Thomas 1982; Amat 1984*a*; Jacobsen 1991; Batt et al. 1992). Some of the apparent differences among species could have been partly the result of differences in the relative proportion of sexes and age-classes, although the same is true of the majority of comparative studies of duck ecology. Data from Spain and Morocco confirm that Marbled Teal feed predominantly at or near the surface throughout the annual cycle, and that upending and diving are rarely observed (Navarro and Robledano 1995; A.J. Green, unpublished data). In the current study, diving was recorded in newly fledged juvenile Marbled Teal but not in adults. Diving was also observed in class IIa (Larson and Taber 1980) ducklings (Green, see footnote 1). Although these observations are of note, given the classification of Marbled Teal within the Aythyini, diving is occasionally observed in a broad range of Anatini (Kear and Johnsgard 1968; Brodsky and Weatherhead 1985). In previous studies, Ferruginous Ducks fed mainly by diving, but upending, head dipping, or bill dipping was frequently observed (Cramp and Simmons 1977; Amat and Soriguer 1982; Dvorak et al. 1996[2]). Pöysä (1983*a*, 1983*b*) found that from May to August, Garganeys fed mainly by gleaning (39%), bill dipping (38%), and neck dipping (17%).

Even when using the same basic feeding method, duck species differ in the duration of feeding events and speed of movement (Eadie et al. 1979). The failure to record the speed of movement of feeding birds in this study underemphasizes the

[2] M. Dvorak, E. Nemeth, S. Tabbich, M. Rössler, and K. Busse. 1996. Bestand, Ökologie und Habitatwahl schilfbewohnender Vogel Arten in der Naturzone des Nationalparks Neusiedlersee-Seewinkel. Unpublished report, BirdLife Austria, Vienna.

extent to which Marbled Teal were more active feeders than Mallards or Garganeys. Whereas the latter two species were almost completely stationary between foraging events, Marbled Teal typically swam almost continuously with the neck outstretched and the head turned down at an angle of ca. 45°, occasionally dipping their bill or head rapidly into the water to take invertebrates near the surface (Green, see footnote 1).

Whereas Pöysa (1983*b*) found a clear separation between diving duck and dabbling duck guilds in both feeding habitat and feeding methods, this was not the case in the current study. The Ferruginous Duck was not ecologically isolated from dabbling ducks in either habitat use or feeding behaviour, and was related to the Mallard along both axes of niche space (Fig. 3). Further work is required to establish if the similarity between these two species is confined to the postbreeding period (e.g., owing to similar requirements during moult). Nor was there any separation between Anatini and Aythyini species in this study. Similarly, Monda and Ratti (1988) found that Ring-necked Duck, *Aythya collaris,* broods showed greater niche overlap with dabbling ducks than with other diving ducks. This shows the importance of studying the two groups simultaneously and brings into question the assumption often made (e.g., Nudds et al. 1981; Nudds 1983; Nudds and Wickett 1994) that dabbling and diving ducks form two neat guilds and that interspecific interactions within them are much more important than those between them.

When more than one resource dimension is considered, competition theory predicts that species similar along one dimension should differ from each other along another dimension (niche complementarity; Schoener 1974; Nudds 1992). Pöysä (1983*b*) found a nonsignificant negative correlation between niche overlaps along the horizontal (feeding habitat) and vertical (feeding methods) axes in a community of ducks, grebes, and coots. Likewise, in the present study, there was a negative correlation between niche overlaps along the horizontal and vertical axes, providing Type II evidence for competition between duck species (see Nudds 1992). Another form of niche complementarity can occur if species feeding in similar ways differ in dietary specialization. Differences in locomotion when feeding are connected with differences in selection of prey items (Eadie et al. 1979; Nudds and Bowlby 1984), and there was a nonsignificant negative correlation ($r = -0.278$, $P = 0.59$) between niche overlap in feeding method/depth (from Table 2) and overlap in feeding mobility (from Fig. 1). The Marbled Teal and Garganey were most similar in feeding method and depth, yet the Marbled Teal was much more mobile (Fig. 1).

This study adds to a growing body of evidence that interspecific interactions have an important influence on niche organization in duck communities (Nudds 1992). The evidence it provides for niche complementarity is not statistically significant, but this is almost inevitable in a community of four species. In any case, in studies where analyses of overlaps among species pairs are significant (e.g., Eadie et al. 1979; Nudds and Wickett 1994), the validity of these statistics is questionable, since the same data for each species are represented repeatedly, causing non-independence. More studies of different duck communities are required to assess whether niche complementarity along the horizontal and vertical axes is a general rule. As far as I am aware, this is the first study of an essentially postbreeding community. Garganeys were only present on postbreeding migration, but in such relatively high numbers that they may potentially impose niche shifts on the species breeding in the Göksu Delta (see Pöysä 1986). Further research is required to compare niche organization during breeding and postbreeding periods in this and other Mediterranean duck communities.

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Appendix

Table A1. Mean morphological measurements (cm) used to calculate feeding depths. Values for the Mallard and Garganey are those used by Pöysä (1983*a*).

	Mallard ($n = 57$)	Garganey ($n = 21$)	Marbled Teal ($n = 8$)	Ferruginous Duck ($n = 8$)
Body length	19.5	15.5	16.0	16.0
Neck length	29.1	18.2	19.8	19.2
Skull length	11.5	7.9	9.0	8.6
Bill length	5.7	3.8	4.5	3.9