
Ecomorphology and coexistence in dabbling ducks: the role of lamellar density and body length in winter

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Ecomorphological differences allow species to coexist within communities, as animals with different morphological characters are likely to use distinct niches, hence reducing interspecific competition. Ecomorphological studies have highlighted the role of e.g. bill size and shape in passerines (Newton 1967), body size in amphibians, reptiles, insects and rodents (Barbault 1992), canine diameter in carnivores (Pimm and Gittleman 1990), neck height and/or incisor arcade structure in herbivorous mammals (Gordon and Illius 1988, Du Toit 1990). Because competition for food has long been a keystone of community ecology, it is not surprising that ecomorphological studies have often focussed on characters related to animal's foraging habits.

Anatidae, especially dabbling ducks (*Anas* spp.), have often been presented as a classic example of how subtle morphological differences may allow congeneric species to coexist (Lack 1971). All *Anas* species are morphologically similar, i.e. broad and elongated body with well-developed neck, and flat bill lined internally with lamellae. However, body length and lamellar density differ between species and these differences have been considered as the means by which duck species can coexist: because dabbling ducks almost never dive to forage, but may have to up-end to reach their food at the bottom of waterbodies, differences in body length allow species to segregate along a foraging depth gradient (Thomas 1982, Pöysä 1983, Pöysä et al. 1994, Green 1998). Ducks use bill lamellae to filter the water or the mud and retain food particles, and differences in lamellar density may allow ducks to segregate along a prey size gradient (Thomas 1982, Nudds and Bowlby 1984, Nudds et al. 1994).

Body length versus lamellar density: controversy and agreement at the Holarctic scale

Several dabbling duck species, such as mallard (*Anas platyrhynchos*), pintail (*A. acuta*), teal (*A. crecca*) and shoveler (*A. clypeata*) are present both in Europe and North America. Surprisingly, in their ecomorphological studies European and North American ecologists have not come to the same conclusion regarding the relative role of morphological characters for the coexistence of these species on their breeding grounds: although a review at the Holarctic scale showed that body mass (and consequently body size) and lamellar densities were comparable in European and North American ducks (Nudds et al. 1994), breeding ducks were observed to segregate along a prey size gradient in the Nearctic (Nudds and Bowlby 1984) while in the Palearctic they mainly differed in their foraging depths (Pöysä et al. 1994). It is only very recently that European and North American ecologists have been able to solve this controversy, by showing that differences in basin shape in the two continents were responsible for this apparent contradiction. Saucer-shaped (i.e. flat) ponds in North America allow all ducks to reach the sediment in most areas, leading species to rely more heavily on differences in lamellar densities (prey size) to reduce interspecific competition (Nudds et al. 2000). Prey size generally decreases from shallow and vegetated (i.e. edges) to deeper (i.e. centre) parts of ponds (Armstrong and Nudds 1985), and duck species utilising differing prey-size classes tend to segregate spatially along a horizontal axis. Conversely, bowl-shaped (i.e. steep) ponds in European breeding grounds allow a

clear segregation of species along a vertical (foraging depth) axis, depending on body length, but no horizontal segregation is possible since all duck species are restricted to a narrow area close to the edges, due to the deepness of pond central areas which makes the bottom out of reach for all species (Nudds et al. 2000).

This Holarctic-scaled hypothesis is very satisfactory, as it resolves what has long been a controversy in ecomorphological patterns and community ecology. In this paper we consider what happens during the wintering season, starting from the point that (i) large species should be able to forage in both shallow and deep water, and (ii) species with dense lamellae should be able to retain both small and large prey items in their bills. We combine behavioural data from a previous study (Guillemain and Fritz 2002) and an original dataset on duck prey sizes to show (1) that despite their ecomorphological differences, sympatric mallard and teal may temporarily use the same foraging depths and prey sizes in early winter, and (2) that the two species subsequently adopt different foraging strategies, relying on either body length or lamellar density and leading to niche divergence from early to late winter within the same foraging areas.

The role of body length: ducks may switch between foraging depths

Wintering dabbling ducks are not restricted to a single, body-size dependent foraging depth. Indeed, most studies have highlighted the great variability of foraging methods that is characteristic of wintering *Anas* (Thomas 1982, Dubowy 1988, Tamisier and Dehorter 1999). There is, however, evidence that dabbling ducks should preferentially select shallow foraging methods (i.e. only the bill submerged, eyes above the water surface), since these provide higher food intake rates and allow them to limit vigilance times through a greater ability to detect predators while foraging (Pöysä 1987, Guillemain et al. 2000, 2001).

In the Reserve Naturelle des Marais d'Yves, in the Marshes of Rochefort, Western France (45°60'N, 01°00'W), scan samples of duck behaviour showed that both mallard and teal foraged predominantly in shallow water at the beginning of winter, but that mallard subsequently switched to deeper foraging (their mean foraging depth [MFD] increased at an increasing rate across weeks: $MFD = 35 \text{ (EXP (0.14 WEEK) + 1) / (EXP (0.14 WEEK) + 49.76) + 4.2}$, $F_{1,21} = 51.37$, $r^2 = 0.71$, $P < 0.0001$), while teal did not ($F_{1,21} = 2.97$, $r^2 = 0.12$, $P > 0.10$; Fig. 1). A vertical segregation, with the smaller species foraging in shallower areas, was thus apparent in the second part of the winter, but not in the first part.

The role of lamellar density: ducks may switch between prey sizes

Although both mallard and teal rely mainly on aquatic invertebrates during the breeding season, both species turn to a granivorous diet in winter (Olney 1963, Dubowy 1988). The size of seeds eaten ranges from 0.5 mm (*Juncus* spp.) to 5.5 mm (*Carex* spp.) for natural seeds (Thomas 1982), but can exceed 1 cm when mallard feed in cultivated fields (Baldassare and Bolen 1984). Here again, there is circumstantial evidence that the two species should share the same preference: experimental studies showed that teal and mallard have higher food intake rates when foraging on larger seeds (Van Eerden and Munsterman 1997) and larger poultry pellets (Fritz et al. 2001), respectively.

We analysed gut contents of 55 mallard and 112 teal provided to us by local hunters. Ducks were shot in the Marshes of Rochefort during the hunting seasons (September–February) 1995–96 to 1998–99. The analysis of gut contents was restricted to the gizzard contents, as the foregut was not always provided. It is known that diets inferred from only gizzard contents may be biased, because soft animal prey and vegetative parts of plants

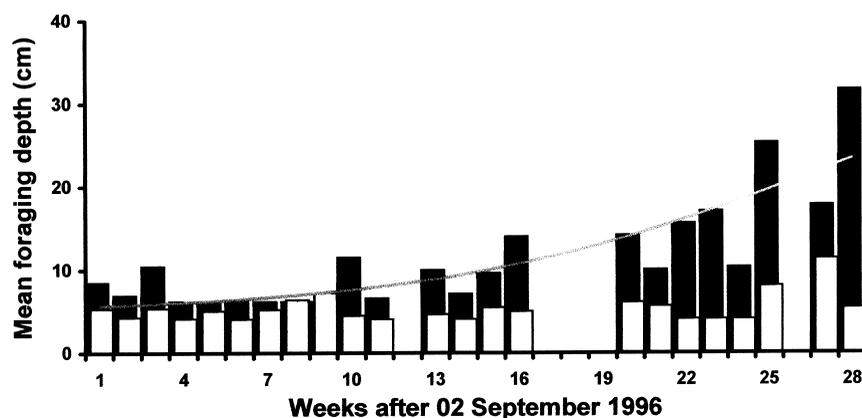


Fig. 1. Mean foraging depth of mallard (black bars, grey curve) and teal (white bars) at Yves during the winter 1996–1997 (data after Guillemain and Fritz 2002). The mean foraging depth of each species was calculated for each study day after the average proportion of birds using a given foraging method and the mean reachable depth by this species using this method (body measurements after Thomas 1982).

Table 1. Occurrence of seeds of each size class in the gizzards of teal and mallard during early and late winter in the Marshes of Rochefort. For each case the first value is the number of gizzards containing seeds of a given size class, and the second value the number of gizzards which did not contain such seeds. NS: $P > 0.05$, *: $P < 0.05$. The significance of each test was adjusted for the number of tests performed following the sequential Bonferroni technique (see text).

Species	Number of gizzards		Chi-square test	
	Early winter	Late winter		
Seed size class I: < 1.5 mm				
mallard	11/27	6/11	$\chi^2 = 0.222$	NS
teal	18/35	38/21	$\chi^2 = 10.351$	*
chi-square	$\chi^2 = 0.256$ NS	$\chi^2 = 4.589$ NS		
Seed size class II: 1.6–3.0 mm				
mallard	34/4	13/4	$\chi^2 = 1.598$	NS
teal	45/8	52/7	$\chi^2 = 0.251$	NS
chi-square	$\chi^2 = 0.403$ NS	$\chi^2 = 1.451$ NS		
Seed size class III: 3.1–4.5 mm				
mallard	12/26	7/10	$\chi^2 = 0.478$	NS
teal	8/45	1/58	$\chi^2 = 6.783$	*
chi-square	$\chi^2 = 3.507$ NS	$\chi^2 = 21.843$ *		
Seed size class IV: > 4.5 mm				
mallard	9/29	4/13	$\chi^2 = 0.000$	NS
teal	1/52	1/58	$\chi^2 = 0.006$	NS
chi-square	$\chi^2 = 10.750$ *	$\chi^2 = 10.237$ *		

are already highly digested in the foregut (Swanson and Bartonek 1970). However, we did not aim to describe the overall diets of the ducks, and the digestion of seeds mainly occurs in the gizzard. We are thus confident that the seed sizes we measured were representative of those actually ingested by dabbling ducks. After being manually sorted from non-digestible (i.e. grit) materials under a binocular magnifying glass, seeds were isolated by species and measured to the nearest 0.01 mm by means of computer software (Cyberview© 5.0) connected to a digital camera. A maximum of 10 different seed species was found per gizzard. Whenever possible, 10 seeds of each species were measured in each gizzard. We compared the frequency of occurrence of seeds of 4 size classes (< 1.5 mm, 1.6–3 mm, 3.1–4.5 mm, > 4.5 mm) in the gizzards of each species during early (Sep–Nov) and late (Dec–Feb) winter using Pearson chi-square tests. Analyses were performed separately for each seed size class. Because the same data were nonetheless used in different tests (i.e. comparison between species within a period of the winter and comparison between periods of the winter within a species), probability values were adjusted following the sequential Bonferroni technique (Rice 1989).

The relative occurrence of seeds did not differ between early and late winter for any size class in mallard gizzards (Table 1). In early winter, the occurrence of seeds differed between mallard and teal gizzards only for the larger ones, i.e. over 4.5 mm, while no significant difference was observed for the other size classes (Table 1). Small seeds of size class I were more fre-

quently found in teal gizzards collected in late winter than in early winter, while the reverse was true for size class III and no significant difference was observed for size classes II and IV (Table 1). In late winter, seeds of size class I tended (although non-significantly) to be more frequent in teal than in mallard gizzards, while the opposite pattern was found for size classes III and IV.

These results show that mallard consumed the same seed sizes throughout the wintering season, while teal switched from sizes very similar to those used by mallard in early winter to much smaller ones in the second part of the season. This indicates that duck species are not always restricted to a single prey size by their lamellar density, and that species such as teal with denser lamellae are able to use both small and large prey. The fact that teal seldom used the very large (and apparently profitable, Van Eerden and Munsterman 1997) seeds (> 4.5 mm) may be because their small bill dimensions restrict their intra-bill cavity and consequently their ability to handle very large food items (Kooloos and Zweers 1991).

Towards a dynamic pattern of segregation in wintering granivorous dabbling ducks

The switch of foraging depth we observed in mallard was not a consequence of a change in water levels across the winter, since these are maintained at fairly

constant levels at Yves by the use of a solar pump. It is also unlikely that teal switched the size of seeds that they used in late winter because very small seeds suddenly became more available: most seeds are readily available to ducks in September (Madsen 1988). In order to ensure that very small seeds were available at the beginning of winter at Yves, we collected 90 mud samples on 9 October 1999, and found *Suaeda fruticosa* (mean size 1.44 mm) in most of the samples containing seeds (i.e. 63 out of 76 samples).

We conclude that dabbling ducks in winter are not restricted to one specific niche by their ecomorphological characters but, rather, show much flexibility in their behaviour. Mallard and teal both seem to follow their own strategy, leading to considerable niche overlap between the two species in early winter, and niche divergence afterwards. It is likely that food depletion is the main cause for the foraging depth/seed size switches that we observed. Both species should first use large seeds in shallow areas, which provide the highest food intake rates, and turn to alternative strategies when these resources become exhausted. As teal have dense lamellae (15.0 cm^{-1} , Nudds et al. 1994) they can switch to smaller seeds while remaining in shallow areas, where they lose less foraging time in vigilance behaviour (Guillemain et al. 2001), while mallard with less dense lamellae (8.0 cm^{-1} , Nudds et al. 1994) would have no choice but to turn to deeper foraging because they cannot feed on small seeds (both for morphological reasons and maybe even because their food intake rate would be too low) (Fig. 2). The pattern we observed corresponds to the Centrifugal community organization described by Rosenzweig and Abramsky

(1986), where the primary preference of all species is shared, but their secondary preferences are distinct. These authors point out that competition should always be a strong dynamical influence in such communities, otherwise no centrifugal niche shifts would be observed. We hypothesise that food depletion is responsible for the observed pattern, but it is not possible at present to test this hypothesis, nor to determine the potential threshold food density under which coexisting mallard and teal turn to divergent strategies. Regular food sampling was unpractical at Yves because the site is a protected area where the disturbance that repeated samplings would cause is not acceptable. As this problem is likely to be widespread in duck wintering quarters, experiments with captive mallard and teal seem to be the most convenient direction for future research; such experiments have already shown, in mallard, that food depletion is indeed responsible for birds switching from shallow to deep foraging (Guillemain et al. 2000). It remains to be established whether depletion of larger seeds also leads teal to concentrate on smaller food items.

Conclusion

While they generally segregate during the breeding season, the results of this study show that dabbling duck species may indeed coexist using the same part of the foraging depth/prey size spectrum during winter. In such a case, mallard and teal appear to select the food and foraging method which previous studies have found to be the most profitable in terms of energy intake and cost of vigilance. Later in the season, and most likely because of food depletion, the two species followed their own and divergent strategies, switching either foraging depth or prey size. Body length and lamellar density then simultaneously contributed to niche segregation.

Our results underline the fact that coexisting species with ecomorphological differences may not always use clearly separated niches, but are likely to share the same resources and simultaneously exploit the same resources, sometimes temporarily. This should especially be the case in guilds of closely-related species, where character displacement often results in only slight morphological differences. In many cases such character displacements would lead to niche enlargement which, although it may provide an ecological refuge to species, does not prevent them from using competitors' niches. This dynamic aspect of community structure should be taken into account by future ecomorphological studies.

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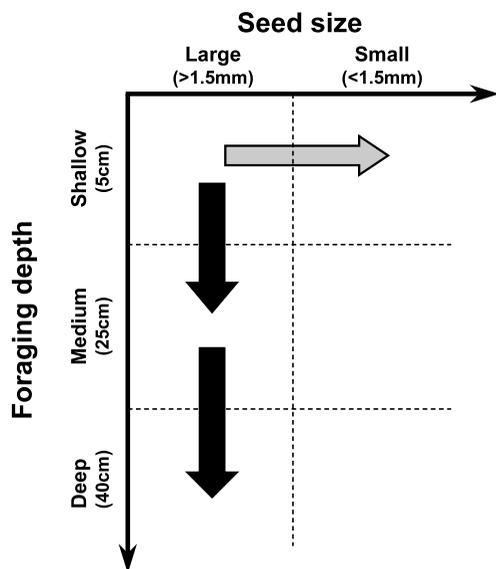


Fig. 2. Niche shifts of mallard (black arrows) and teal (grey arrows) in response to food depletion. Arrows show behavioural and diet shifts observed in this study.

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