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Temporal variation in feeding tactics: exploring the role of competition and predators in wintering dabbling ducks

Matthieu Guillemain & Hervé Fritz

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To evaluate the effects of competition and predation on foraging by wintering granivorous dabbling ducks, we collected data on long-term changes in foraging methods used during winter in the marshes of western France. Teal *Anas crecca*, mallard *A. platyrhynchos* and pintail *A. acuta* start feeding in shallow areas, and later switch to deeper feeding methods. We show experimentally that the food intake rate is 1.5 times higher in shallow (5 cm) than in deep (35 cm) areas, which may explain why shallow feeding is the principal method used early in the winter season. In the field, the switch between foraging methods was neither related to the frequency of fly-overs by raptors nor to the density of competitors at a foraging site, although birds foraged deeper sooner at sites frequented more often. Thus, the potential role of interference competition remained unclear. Conversely, at each site, the proportion of deep foragers increased with increasing cumulative numbers of foragers, used as a measure of food depletion. We therefore have no evidence that disturbance by predators has an important effect on the foraging methods used, whereas competition through food depletion may play a major role.

Key words: *Anas* sp., competition, foraging, predation, winter

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Food resources are generally distributed heterogeneously, both in time and space, and foraging animals show flexible responses to this heterogeneity. This flexibility is expressed at different levels: animals can turn to

a new habitat, select a different patch within a habitat, and select different items within a patch (reviews in Stephens & Krebs 1986, Hughes 1993, Sutherland 1996).

Another type of behavioural adjustment involves switching search methods (Stephens & Krebs 1986). An animal may have several search tactics: no less than 15 different foraging methods have been identified by Recher, Holmes, Davis & Morton (1983) in eastern reef heron *Egretta sacra*. The switch from 'sit and wait' to 'active search', or the variable sinuosity of search tracks ('random walk' versus 'directed movement') has also been the subject of numerous studies (e.g. Thomas 1974, Davies 1977, Formanovicz & Bradley 1987, Grant & Noakes 1987, Village 1990, Bell 1991, Nakano, Fausch & Kitano 1999). Longer-term changes of foraging behaviour have often been ascribed to effects of competition, either interference competition (Goss-Custard 1980, Sutherland & Koene 1982, Ens & Goss-Custard 1984, Norris & Johnstone 1998) or food depletion (Székely & Bamberger 1992, Sutherland & Anderson 1993, Sutherland & Allport 1994).

Most studies of behavioural flexibility in response to competition have focused on spatial aspects: individuals will turn to alternative patches with lower resource abundance to avoid the negative effects of interference at high density of competitors in the best patches (e.g. subdominant oystercatchers *Haematopus ostralegus* that turn to less profitable mussel beds; Goss-Custard, Clarke & Durell 1984). Depletion studies are generally concerned with habitat or patch selection, whether changes are linked to a change in the diet or not (e.g. brent geese *Branta bernicla* that switch from *Zostera* beds to salt-marshes and then agricultural fields through the winter; Charman 1979, Percival, Sutherland & Evans 1996; or oystercatchers that increase the range of the mussel beds they use to compensate for the depletion of the best ones; Goss-Custard, West & Sutherland 1996).

Long-term changes in searching methods across the winter have been documented in dabbling ducks, but they were linked to variations in the physical characteristics of the feeding patches (i.e. levels of flooding) rather than to competition for food (Thomas 1982). In the context of optimal foraging, Pöysä (1989) showed that the ability to change between methods in the course of the day (i.e. to switch from shallow to deep foraging) allows teal *Anas crecca* to increase patch residence time by using more of their invertebrate prey in the water column in summer. The same type of result has been reported for wintering northern shoveler *Anas clypeata* foraging on zooplankton (Guillemain, Fritz & Guillon 2000b). Several dabbling ducks, e.g. teal, mallard *A. platyrhynchos* and pintail *A. acuta*, become almost entirely granivorous during the winter (e.g. Thomas 1982, Tamisier & Dehorter 1999). They do not feed in the whole water column as they do in summer, but search for seeds in the

sediments of waterbodies. A major difference between the two seasons is that, in winter, granivorous birds are restricted to one foraging method per patch which depends on water levels, i.e. shallow or deep patches, while several behaviours are possible within one patch in summer as the birds forage on animal prey in the whole water column. In addition to these facts, several points strongly suggest that wintering dabbling ducks make up good models to test hypotheses about the mechanisms involved in switches between foraging methods:

- Their foraging methods, from grubbing to up-ending (Thomas 1982) fall into two very different categories: shallow feeding where their eyes are above the surface, and deep feeding where their eyes are under water. The latter category is thought to provide lower intake rates due to more frequent interruptions of feeding (Guillemain, Fritz & Blais 2000a, Guillemain, Duncan & Fritz 2001), in response to greater predation risk when ducks cannot visually detect predators (Pöysä 1989);
- Disturbance by predators is frequent in French wintering areas (e.g. Tamisier 1972, Fritz, Guillemain & Guérin 2000), and therefore ducks may refrain from using the riskier deep feeding;
- Wintering ducks often aggregate in very large numbers in limited areas (Zwarts 1976, Scott & Rose 1996), which is likely to increase competition processes; and
- Winter flocks are usually plurispecific, which offers the possibility to compare search tactics in species with different morphology.

As part of a long-term study of ducks wintering in the marshes of western France, we sought to identify causes for switching between foraging methods and test hypotheses about the mechanisms involved in the decisions made by individuals of three granivorous duck species. Field observations were carried out in protected areas where constant water levels are maintained, but the depth of the patches varies with the topography of the waterbodies. In this paper, using an extensive data set from field observations and laboratory experiments, we:

- show that the three species are mainly granivorous during winter in this part of France;
- describe changes in feeding methods over the course of winter;
- test experimentally whether the principal feeding method provides the highest intake rate; and
- explore in the field whether interference competition and food depletion may lead to ducks switching from shallow to deep foraging and, conversely, if disturb-

ance by predators prevent this switch from safer to riskier methods.

Methods

Foods consumed by wild dabbling ducks

The winter diets of dabbling ducks were analysed using gizzard contents collected from ducks shot by local hunters in the Département of Charente-Maritime during the wildfowling seasons (mid-September - 28 February) 1995/96 to 1997/98. Soft items of small size, especially planktonic invertebrates, are rapidly broken down in gizzards (Swanson & Bartonek 1970). Diet analyses of food items (requiring the determination of prey species) based on gizzard rather than gizzard and proventriculus contents can thus lead to biased results, especially during the breeding season when most species rely on soft invertebrates (Nudds & Bowlby 1984). However, the aim of our analysis was not to determine prey species, but to measure the relative amount of seeds, animal prey and vegetative material in the overall diet in winter. The analysis of gizzard contents should thus provide reliable data. Gizzards were stored frozen by hunters to avoid post-mortem digestion (Swanson & Bartonek 1970) and their contents were hand-sorted in the laboratory under a binocular microscope, dried for 24 hours at 80°C and weighed. Relative dry weights (i.e. dry weight of a particular food type expressed as a percentage of the total dry weight of all food items in each gizzard) of the three types of food were calculated.

Most of the ducks (63%) were collected in the early part of the night, between 17:00 and 00:00, on arrival at their nocturnal foraging habitats. The food samples should thus be representative of what dabbling ducks ate on day-roosts like our study sites.

Experimental measures of intake rate

Our experiments were carried out in April-May 1999 at the Centre d'Etudes Biologiques de Chizé (60 km east of La Rochelle), on nine captive mallard (three males and six females). Each day over a 10-day period, individuals were randomly split in three groups of three individuals (one male and two females; Guillemain et al. 2000a). One group was given food (in the form of 100 grams of wheat) at a water depth of 5 cm, the second group had wheat at 35 cm. The wheat was oven-dried for 24 hours at 60°C before presentation to the ducks, dispersed in a 2-m² pool and covered by approximately 2 mm of fine sand (3 kg.m⁻²) to resemble natural conditions. The behaviour of each individual was recorded every five minutes from 09:00 to 12:00 to measure the

total time spent feeding. The food that had not been eaten was collected at the end of the experiment, oven-dried for 24 hours at 60°C and weighed. The quantity eaten and the average individual intake rate (in grams per minute of feeding) per group of three birds were calculated. At the end of the experiment, ducks were released and could feed *ad libitum* on poultry pellets. The ducks were deprived of food the night before an experiment.

Feeding behaviour in the field

Data were collected during September 1996 - March 1997 on two sites of the Rochefort marshes, in the department of Charente-Maritime, western France (45°60'N, 01°00'W): the Nature Reserve of Yves (hereafter Yves) and the municipal sewage works of Rochefort, which consists of a biological treatment process in large waterbodies, where hunting is prohibited (hereafter Stepro). A binocular (x4) light amplifier (Thompson Optronique UGO) was used for nocturnal observations.

The study site at Yves was a 24-ha waterbody separated from the Atlantic Ocean by a sea wall and its water level is maintained roughly constant by the use of a solar pump. The maximum depth is about 35 cm. At Stepro, ducks were observed on a 6.5-ha pond which receives water from the sewage treatment works and overflows into the river Charente, so water levels here also remained nearly constant at a maximum depth of about 30 cm, except in a circular ditch where it reached 2 m. Each site was visited one day a week for observations. The two sites differed in the number of dabbling ducks they hosted (Table 1). Yves was a typical day-roost, with a density of ducks much higher during the day than during the night. Although Stepro was also used more heavily during the day than during the night, differences in duck numbers in the two periods were less pronounced than at Yves.

Scan sampling of flock behaviour (Altmann 1974) was

Table 1. Densities (number.ha⁻¹) of mallard, teal and pintail at Stepro (6.5 ha) and Yves (24 ha), during daylight hours and during the night. Values are means $\pm$ SE, calculated over average data from each study day. Trends in densities across weeks are presented in parentheses*. Comparisons of duck densities** during daylight hours and during the night were not performed for pintail at Stepro due to their occasional presence.

	Daylight hours (N = 25)	Night (N = 18)	Significance of differences between day/night	
Stepro				
Mallard	1.7 $\pm$ 0.2 (-)	2.5 $\pm$ 0.6 (-)	t = -1.47	ns
Teal	15.1 $\pm$ 1.7 (ns)	8.6 $\pm$ 1.7 (-)	t = 2.72	P < 0.01
Pintail	Occasional	Occasional	-	-
Yves				
	(N = 23)	(N = 19)		
Mallard	9.2 $\pm$ 1.2 (-)	0.7 $\pm$ 0.5 (ns)	t = 6.18	P < 0.0001
Teal	5.9 $\pm$ 0.7 (ns)	0.2 $\pm$ 0.1 (ns)	t = 7.46	P < 0.0001
Pintail	2.5 $\pm$ 0.5 (+)	0 $\pm$ 0.1	t = 4.83	P < 0.0001

* Spearman correlations, P < 0.05.

** Student's bilateral t-tests.

performed each week on each site throughout daylight hours (i.e. generally between 07:00 and 18:00). On average, seven scans were performed per day at Stepro, and six at Yves. This gave the total number of ducks as well as the activity of each individual (e.g. foraging and resting), allowing the calculation of an average time-budget for each duck population. In particular, this gave the number of foraging individuals and, among them, the proportion of deep foraging birds (i.e. foraging with head and neck underwater or by up-ending). The proportions were arcsine-transformed before statistical analyses (Sokal & Rohlf 1995). Note that the sample sizes of foraging data can be lower (and can differ between species) than the number of scan samples, since, in some scans, no birds of a particular species may have been feeding. As the ducks were not individually marked, it was not possible to assess the degree to which successive scan samples were statistically independent. However, we are confident that potential pseudoreplication was limited since (i) only average weekly data were included in the analyses, and (ii) Pradel, Rioux, Tamisier & Lebreton (1997) showed rapid turn-overs of individuals in wintering dabbling duck populations in France.

Interference

Interference was studied on a weekly basis at each site by plotting the average proportion of deep foragers against the average density of foraging individuals on that study day. The crude density of birds, i.e. feeding plus non-feeding, was irrelevant since non-foraging birds were roosting or preening on islets and on the dry banks of the waterbodies, and were therefore unlikely to interfere with ducks foraging in either shallow or deep water. Some authors studied interference by plotting aspects of foraging behaviour (used as indicators of intake rate) on foraging group size or distance from neighbour, as a measure of forager density within close range (e.g. Pöysä 1987). This also was irrelevant in our case, as shallow and deep foraging take place at distinct places: it is thus unlikely that a whole foraging group would move when additional individuals join the flock and/or the distance from neighbours decreases.

Analyses were run for each species with both the density of foraging conspecifics and the density of foraging granivores, because both intraspecific and interspecific competition have been found in dabbling ducks (Pöysä 1986). This analysis tests for an interference process similar to the buffer effect described by Brown (1969) and observed by Zwarts (1976) in teal, i.e. a saturation of the best patches leading to some individuals being forced to less profitable (in this case, deeper) areas when density increases.

Food depletion

Regular measurements of the food resources available at each site were not possible because this would have caused repeated disturbance in the protected areas, a common problem in studies of such birds which necessitates the use of indirect measures of food abundance and depletion (e.g. Pöysä 1989). Because seeds can be considered as non-renewable food sources during the winter, the cumulative number of foraging ducks was used as an index of the amount of seeds removed throughout the season in order to study the effect of depletion. Values were calculated from average daily numbers of foragers, including nocturnal data, to incorporate the differential use of the two sites during the night. Values are expressed as foraging duck days. Only teal and mallard data were analysed at Stepro because pintail were observed on only two occasions. All three species were considered at Yves.

Influence of predator disturbance

Dabbling ducks wintering in western France suffer very low predation during daylight hours, but fly-overs by raptors may induce anti-predator responses by ducks and thus induce important disturbances in foraging (Fritz et al. 2000). Fly-overs by raptors were recorded during our observations. The appearance of each buzzard *Buteo buteo*, marsh harrier *Circus aeruginosus* and peregrine *Falco peregrinus* was noted, allowing the calculation of the frequency of fly-overs (in numbers.min⁻¹) for each day of observation. The relationship between this frequency and the proportion of deep foraging ducks was examined in each species and site to assess if variations in the predator disturbance could explain the patterns of switching between foraging methods across the winter.

Results

Diets of dabbling ducks in the study area

Of the 149 gizzards provided by hunters, 11 were empty or only contained a mixture of heavily digested non-identifiable materials, and these were not included in the analyses. The remaining 138 gizzards came from 79 teal, 45 mallard and 14 pintail. As expected, the three species were mainly granivorous in Charente-Maritime during the winter, as seeds accounted for 91.2% (± 2.4 SE) of the diet in teal, 83.6% (± 4.2 SE) in mallard and 59.2% (± 11.8 SE) in pintail. Animal prey and vegetative material were of minor importance for mallard and teal, whereas animal prey represented 25.4% (± 11.3 SE) of the diet in pintail.

Experimental measures of intake rate

Mallard had higher instantaneous food intake rates in shallow than in deep water (0.99 ± 0.12 SE and 0.60 ± 0.07 SE g.minute feeding⁻¹.individual⁻¹, respectively, $N = 10$ in both cases; Mann-Whitney: $U = 80.00$, $P < 0.05$).

The time spent on feeding activities did not differ whether birds were feeding in shallow or deep water (26.33 ± 3.73 SE and 34.33 ± 2.90 SE minutes per individual, respectively, $N = 10$ in both cases; Mann-Whitney: $U = 24.50$, $P > 0.05$).

Switches between searching methods through the winter

The search methods of granivorous dabbling ducks changed through the winter, with an increase in the use of deep foraging across weeks (Fig. 1). This pattern was observed in all species at both sites, although the trend was just above the significance threshold for teal at Yves (Linear regression: $F_{1,21} = 3.60$, $P = 0.0715$). At this site, no mallard or pintail fed in deep water at the beginning of the season, and the proportion of deep foragers subsequently increased rapidly. These data fitted a sigmoid equation of the form: mallard: $Y = 90$

Table 2. Diurnal proportion (foraging activity) and density of foragers at Stepro and Yves. Values are means $\pm$ SE, calculated over average data from each study day. Comparisons between the sites were performed using Student's bilateral t-tests.

	Stepro (N = 25)	Yves (N = 23)		
Proportion of foragers				
All granivores	0.48 ± 0.03	0.07 ± 0.01	$t = 13.27$	$P < 0.0001$
Mallard	0.30 ± 0.03	0.04 ± 0.01	$t = 10.53$	$P < 0.0001$
Teal	0.52 ± 0.03	0.17 ± 0.04	$t = 7.22$	$P < 0.0001$
Pintail	-	0.05 ± 0.01		
Density of foragers (number.ha ⁻¹)				
All granivores	8.50 ± 1.01	1.03 ± 0.19	$t = 6.98$	$P < 0.0001$
Mallard	0.48 ± 0.07	0.22 ± 0.06	$t = 2.84$	$P < 0.01$
Teal	7.97 ± 1.00	0.74 ± 0.16	$t = 6.86$	$P < 0.0001$
Pintail	-	0.06 ± 0.01		

($\exp(0.21x) - 1) / (\exp(0.21x) + 180.89)$, $F_{1,21} = 54.99$, $r^2 = 0.72$, $P < 0.0001$; pintail: $Y = 90 (\exp(0.20x) - 1) / (\exp(0.20x) + 64.97)$, $F_{1,14} = 36.95$, $r^2 = 0.73$, $P < 0.0001$. At Stepro, the proportion of deep foraging teal and mallard increased linearly across weeks ($Y = 22.49 + 1.22x$, $F_{1,23} = 11.39$, $P < 0.01$, $r^2 = 0.33$ and $Y = 40.12 + 1.21x$, $F_{1,23} = 7.42$, $P < 0.05$, $r^2 = 0.24$ respectively). In both species the y-intercept value differed significantly from zero (teal: 22.49 ± 5.93 SE, $P < 0.001$; mallard: 40.12 ± 7.31 SE, $P < 0.0001$), showing that mallard and

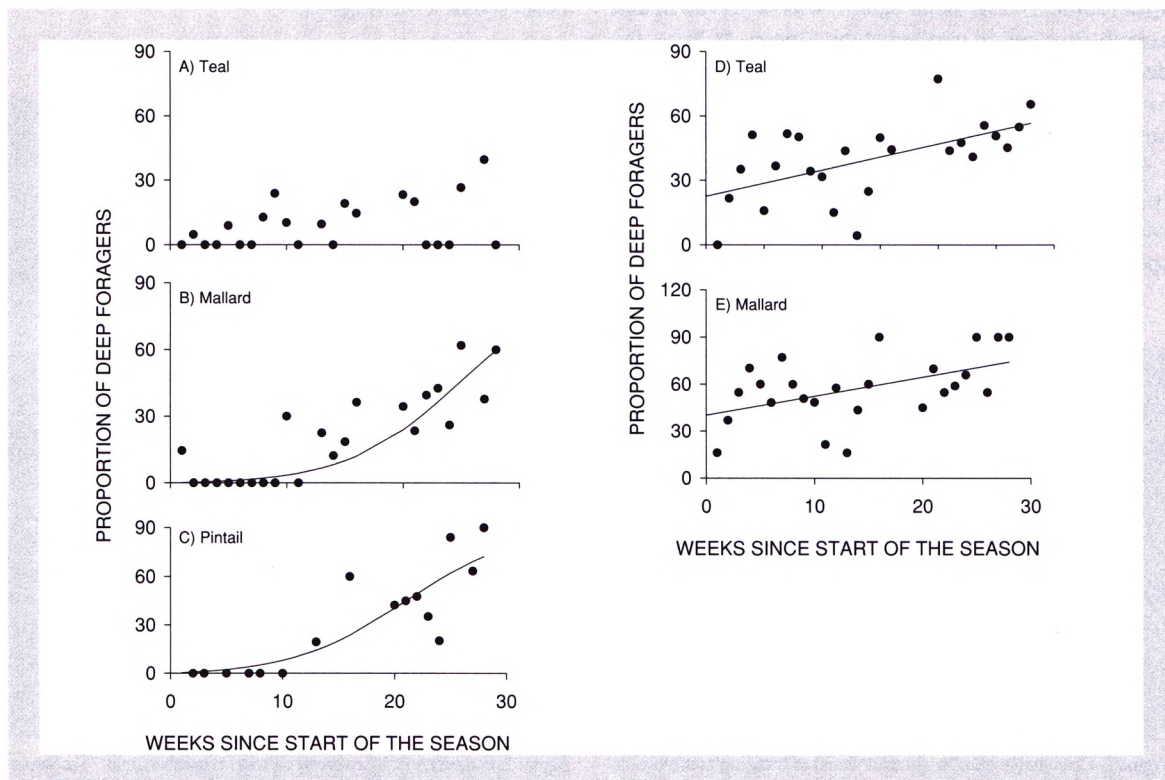


Figure 1. Proportion (arcsine-transformed) of deep foraging individuals of teal, mallard and pintail according to weeks after the start of the season (mid-September 1996 - March 1997) at Yves (A-C) and Stepro (D-E), France. See text for statistics.

Table 3. Trends in forager density at Yves and Stepro during mid-September 1996 - March 1997. Analyses were performed on average weekly data.

Yves					
All granivores	Y = 1.89 - 0.06 WEEK	F _{1,21} = 12.62	r ² = 0.38	P = 0.0019	
Mallard	-	F _{1,21} = 2.42	r ² = 0.10	P = 0.1350	
Teal	Y = 1.54 - 0.06 WEEK	F _{1,21} = 17.52	r ² = 0.45	P = 0.0004	
Pintail	Y = -0.01 + 0.001 WEEK	F _{1,21} = 17.31	r ² = 0.45	P = 0.0004	
Stepro					
All granivores	Y = 12.32 - 0.27 WEEK	F _{1,23} = 6.29	r ² = 0.21	P = 0.0197	
Mallard	Y = 0.90 - 0.03 WEEK	F _{1,23} = 32.43	r ² = 0.59	P < 0.0001	
Teal	Y = 11.41 - 0.24 WEEK	F _{1,23} = 4.93	r ² = 0.18	P < 0.0365	
Pintail	-	-	-	-	

teal already fed deeper at Stepro than at Yves at the beginning of winter.

Competition parameters and predator disturbance through the winter

The higher proportion of foraging individuals at Stepro shows that this site was used more heavily as a feeding habitat than Yves (Table 2). This, and the smaller size of the study site at Stepro, led the densities of foraging individuals to being much higher than at Yves (see Table 2). The overall density of foragers (i.e. the three species altogether) decreased across weeks at the two sites (Table 3). The same pattern was observed in teal at both sites and in mallard at the Stepro. At Yves, the density of foraging pintail increased through the winter whereas the density of foraging mallard did not show any significant trend across weeks (see Table 3).

The cumulative number of foragers increased fairly steadily over time at both sites, except from late December to the middle of January because a cold spell led the sites to being covered with ice, prevent-

ing foraging for most of the ducks. An ANCOVA with SITE as a factor and WEEK as a covariate showed that the rate of increase of the cumulative number of foragers across weeks was higher at Stepro than at Yves (SITE $\times$ WEEK: $F = 346.50$, $P < 0.0001$; Fig. 2), reflecting the fact that Stepro is more heavily used as a foraging habitat by dabbling ducks than is Yves.

The average frequency of raptor fly-overs did not differ between Stepro and Yves (i.e. 0.064 fly-overs per minute ± 0.011 SE and 0.057 ± 0.009 SE; $t_{19,17} = -0.17$, $P > 0.05$), but it decreased markedly at Stepro across the winter, whereas a marginally significant trend was observed at Yves (Fig. 3).

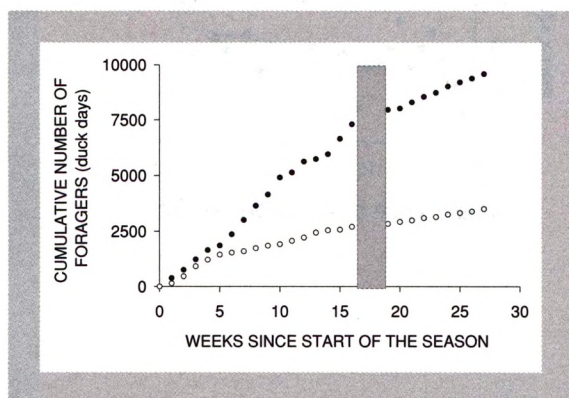


Figure 2. Cumulative number (in duck days) of foraging granivores at Stepro (●) and Yves (○) according to weeks after the start of the season (mid-September 1996 - March 1997). The grey area represents the period when sites were frozen due to a cold spell. See text for statistics.

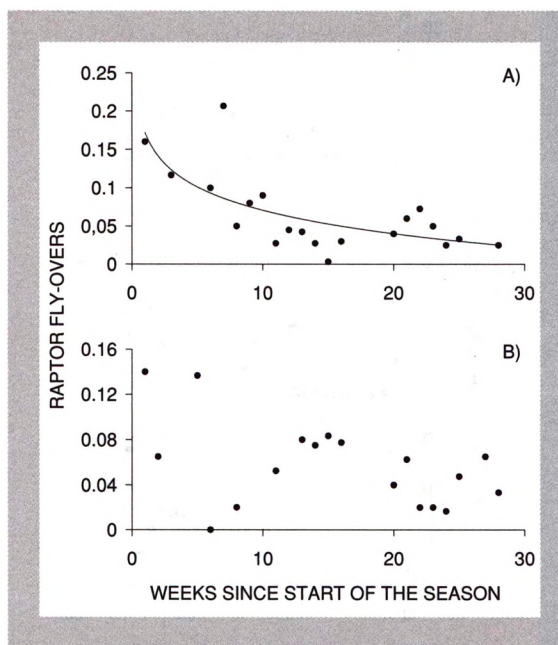


Figure 3. Frequency of fly-overs by raptors (in numbers.min.⁻¹) at Stepro (A; $Y = 0.17 - 0.04 \text{ Ln}(X)$; $F_{1,18} = 18.05$, $r^2 = 0.50$, $P = 0.0005$) and Yves (B; $F_{1,16} = 4.22$, $P = 0.0566$) according to weeks after the start of the season (mid-September 1996 - March 1997).

Table 4. Results of a backwards step-by-step multivariate regression of the proportion of deep foraging teal, mallard and pintail at Stepro and Yves on the density of foraging conspecifics, the overall density of foraging granivores, the cumulative number of foragers (CUMFOR)* and the frequency of raptor fly-overs at each site. Only final models are presented (see text for further explanation).

			F	df	r ²	P
Stepro						
Teal (N = 25)	Model	(CUMFOR)	9.68	1	0.30	P < 0.01
Mallard (N = 25)	Model	(CUMFOR)	5.44	1	0.19	P < 0.05
Yves						
Teal (N = 23)	Model	(CUMFOR)	3.81	1	0.15	P < 0.07
Mallard (N = 23)	Model		37.36	2	0.79	P < 0.0001
		CUMFOR	3.94	1	0.19	ns
		CUMFOR*CUMFOR	17.20	1	0.81	P < 0.0001
	Model		22.58	2	0.78	P < 0.0001
Pintail (N = 16)		CUMFOR	1.16	1	0.15	ns
		CUMFOR*CUMFOR	6.71	1	0.85	P < 0.05

* Note that due to the non-linearity of the relationship, CUMFOR was included in the model as a quadratic for mallard and pintail at Yves.

Relative importance of interference, depletion and predator disturbance

A backward stepwise multivariate regression, including the density of foragers, the cumulative number of foragers and the frequency of raptor fly-overs for each duck species at each site highlighted the role of depletion on the selection of a foraging method by dabbling ducks: the frequency of raptor fly-overs and the density of foragers never explained a significant proportion of the variance; these variables were therefore removed. In all five cases, the best fitting model included only the cumulative number of foragers (Table 4), and was positive. Only in teal at Yves was the final mod-

el marginally significant, although the trend was the same and only the cumulative number of foragers remained. Another consequence of increases in the cumulative number of foragers was a gradual decrease of the proportion of foraging individuals, with all species combined, both at the Stepro ($Y = 51.10 - 0.001x$, $F_{1,23} = 6.74$, $P < 0.05$, $r^2 = 0.23$) and at Yves ($Y = 19.63 - 0.003x$, $F_{1,21} = 17.15$, $P < 0.001$, $r^2 = 0.45$; Fig. 4).

Discussion

Long-term switches in foraging methods

For the three species, at both sites, the principal foraging method at the beginning of winter was foraging with only the bill submerged, and the ducks switched to deep foraging methods in the latter part of the season. This pattern is consistent with the results of a previous study showing that mallard had a strong preference for shallow rather than deep foraging patches in standardised experimental conditions (Guillemain et al. 2000a). Short-term switches between search tactics have already been described in a wide range of animals as a way of adapting rapidly and reversibly to varying foraging conditions (e.g. Recher et al. 1983, Thomas 1974, Davies 1977, Formanovicz & Bradley 1987, Grant & Noakes 1987, Village 1990, Bell 1991, Nakano et al. 1999). In our case, however, search methods varied in the long term, which may have major consequences for the foraging efficiency of individuals, especially with respect to the risk of predation (see also Cézilly & Boy 1988): deep foraging ducks cannot detect an approaching danger as their eyes are underwater, while their body is still visible to predators (Pöysä 1987). In order to compensate for this, deep foragers shorten their feeding bouts and have more fragmented feeding sessions (Tamisier 1972, Guillemain et al. 2001), which may affect their food intake rate. However, none of the species showed a decrease in use

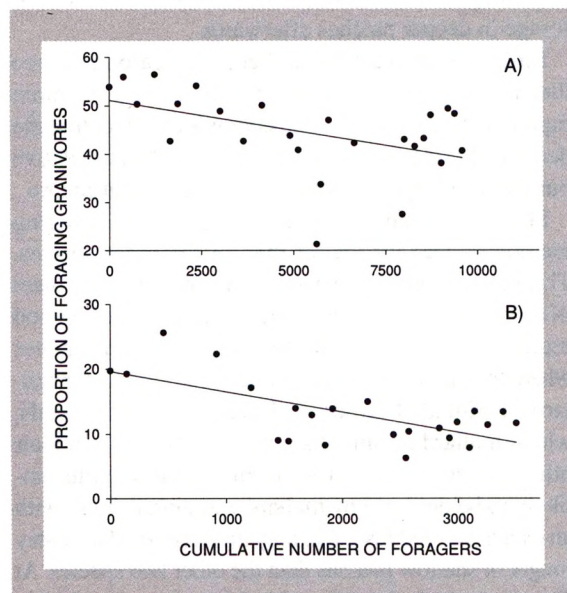


Figure 4. Relationship between the proportion (arcsine-transformed) of foraging granivores and the level of food depletion, measured and expressed as the cumulative number (in duck days) of foraging individuals at Stepro (A) and Yves (B). See text for statistics.

of deep foraging with increases in the frequency of flyovers by raptors. We conclude that predator disturbance does not seem to be a major factor governing the selection of foraging methods by dabbling ducks. This does not mean that these birds are insensitive to predation risk: predation may affect either their overall time-budget (i.e. their decision to feed at all; Fritz et al. 2000), or the structure of their foraging behaviour, the length of feeding bouts or the frequency of vigilance episodes (McVean & Haddlesey 1980, Guillemain et al. 2001).

Potential role of competition in the switch of foraging methods

In laboratory experiments mallards have 1.5 times higher food intake rates when feeding at a depth of 5 cm than when feeding on deep food at 35 cm. It is widely assumed that the intake rate of dabbling ducks decreases with increasing depth (e.g. Pöysä 1989), and a previous study supported this idea (Guillemain et al. 2000a). However, this is to our knowledge the first time that a set of laboratory experiments has been especially designed to compare food intake rates of shallow and deep feeding ducks. The results clearly show that shallow foraging provides a higher return.

Interference competition

No species at either of the two sites increased their use of deep patches in relation to the density of competitors, either intra- or interspecifically. The role of interference on individual foraging behaviour has been demonstrated in several studies, but these have been of species feeding on conspicuous prey with long handling times, which is likely to promote kleptoparasitism (e.g. oystercatchers feeding on mussels *Mytilus edulis* (Ens & Cayford 1996), gadwall *Anas strepera* robbing vegetative materials from coot *Fulica atra* (Amat & Soriguer 1984)). Our empirical data on dabbling ducks' foods confirm that teal, mallard and pintail are mainly granivorous during winter in western France (see also Olney 1963, Thomas 1982, Pirot, Chessel & Tamsier 1984), and are therefore unlikely to suffer from kleptoparasitism (Brockmann & Barnard 1979).

Interference could also occur through saturation of the best patches, or through aggressive behaviour by dominant birds, forcing others to less profitable areas (e.g. Harper 1982, Goss-Custard et al. 1984, Milinski & Parker 1991). Since seeds in the sediment generally occur at low densities (e.g. Tamsier & Dehorter 1999, Guillemain, Houte & Fritz 2000c), it is unlikely that birds could defend a seed patch *per se*, but the birds have higher intake rates in shallow water, which should therefore be saturated first, and could be defended by

dominants. The lack of a significant relationship between the use of deep patches and the density of competitors at the two sites may be linked to the low densities recorded in this study (< 10 feeding birds.ha⁻¹), since Zwarts (1976) only observed interference when densities were above 250 feeding teal per ha. However, interestingly, at Stepro where the density of foragers was higher the granivorous dabbling ducks used deep foraging methods more intensely and earlier in the season than at Yves. Our results thus provide some indirect evidence for the operation of interference, which would require further testing through the analysis of the behaviour of ducks on a larger number of foraging sites.

Depletion

Virtually no pintail or mallard foraged deeply at Yves before a threshold cumulative number of foragers had been reached. This avoidance of deep foraging methods suggests that when a choice is possible, shallow foraging is preferred by wild ducks (see also Guillemain et al. 2000a). At Stepro, the proportion of individuals using deep patches increased with the cumulative number of foraging granivores, suggesting that food depletion may have been a major factor affecting the birds' behaviour. It is known from previous studies that duck consumption can affect the standing crop of food over the winter period (Miller 1985, Madsen 1988, Tamsier & Dehorter 1999, Guillemain et al. 2000c). It is thus likely that ducks depleted seeds from shallow areas at the beginning of the season, which constrained them to forage in deeper patches afterwards.

Birds used deep patches earlier in the season at Stepro than at Yves, suggesting that depletion occurred more rapidly there, which is consistent with the fact that the density of foragers was higher, and that the cumulative number of foragers increased more rapidly at Stepro.

Shallow feeding remained the principal foraging method of teal for longer than in the other species. This pattern could be due to the fact that the body mass of teal is a third that of mallard, so teal have smaller food requirements and should be able to exploit patches where food availability and intake rate is too low for mallard or pintail. Further, teal feed on smaller seeds, which mallard or pintail are not able to retain in their bill lamellae (Thomas 1982): small seeds are thus unlikely to be depleted by mallard and pintail. Teal, with an exclusive food resource, may therefore be able to stay longer in shallow patches than the other two species. At Stepro, the high densities of teal may have resulted in a more rapid depletion of the small seeds, leading to teal switching to deep foraging as quickly as mallard at this site. Food depletion thus seems to play a major role

in the choice of foraging methods in granivorous dabbling ducks in this wintering area.

In conclusion, our study shows that switching between search methods is not only a short-term, and reversible, adjustment to fluctuating feeding conditions, but can also be a long-term change which allows foragers to adapt to long-term changes in feeding conditions. We found no evidence for an effect of disturbance by predators on the choice of foraging methods, and obtained conflicting results for the role of interference depending on whether this factor was considered within or between sites. Food depletion, on the other hand, appears to play a major role. It would be worth exploring this further by making direct measurements of spatial and temporal variations in food resources, combined with measurements of feeding strategies. In nature reserves where an objective is to favour wintering ducks, many managers have, empirically, chosen to maintain large areas of open shallow water. Our results provide a biological explanation as to why open shallow waters are attractive to granivorous dabbling ducks.

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