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Foraging strategies of granivorous dabbling ducks wintering in protected areas of the French Atlantic coast

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Abstract. Most important day-roosts for wintering ducks are protected, but the use of such sites as foraging habitats by Anatidae has received little attention. We studied the foraging activity of wintering mallard (*Anas platyrhynchos*) and teal (*A. crecca*) at four protected areas of the Marshes of Rochefort, western France. These species are generally nocturnal feeders, but they may expand their foraging time into the daylight hours if they have high energy requirements. Our goal was to identify the factors that lead dabbling ducks to increase their daily foraging time, so that the management of protected sites used by ducks diurnally could be adjusted accordingly. We demonstrate for the first time that, at the holarctic scale, granivorous ducks in colder habitats have longer diurnal foraging times. In western France, foraging represented 37–60% of ducks' daily time-budget: 16% of daylight hours and 85% of the night were spent foraging on average. Teal (350 g) fed longer per day than mallard (1100 g), and this seemed to result from different migration strategies rather than differences in body mass. This study suggests that management of protected areas should be adjusted to the climatic conditions of a wintering quarter and to the migration status of species in the duck community, so that adequate foraging sites are available for energetically stressed individuals to fulfil their daily requirements.

Introduction

Ducks and geese often serve as flagship species for wetland conservation, and most important wintering areas for ducks and geese are protected. Among the 256 sites of international importance for dabbling ducks in Africa and western Eurasia, 190 (74%) are protected to at least some extent (Scott and Rose 1996). The feeding ecology of wintering granivorous dabbling ducks (*Anas* spp.) has been intensively studied in the Camargue, south of France, where the birds feed very little by day (<10%) and at night fly far from roosts to a variety of feeding habitats (e.g. freshwater marshes and rice fields; Tamisier 1976, 1978). Further, their foraging strategy varies across the winter period, with the greatest investment in feeding after the autumn and before the spring migrations. In mid-winter, the birds invest less time in foraging, and more in pair formation (the *wintering strategy*; Tamisier et al. 1995). The extent to which these principles also apply for birds in more northerly winter quarters is not known, but several authors have hypothesised that wintering

dabbling ducks in northern sites should feed more during daylight hours, as their energy requirements are greater due to colder temperatures (Tamisier 1972a; Paulus 1988; McNeil et al. 1992).

As part of a wider study of the ecology of wintering ducks in the western marshes of France, we have obtained detailed information on the foraging strategies of northern shoveler *Anas clypeata* (Guillemain et al. 2000b). Here we present data on the two commonest granivorous species, teal *A. crecca* and mallard *A. platyrhynchos*. We test the following hypotheses for ducks in this Atlantic winter quarter:

1. that they feed for more of the day than birds further south, in warmer areas such as the Camargue,
2. that teal (350 g) have longer feeding times than mallard (1100 g), as expected from the relationship between body-mass and foraging time in Anatidae (Mayhew 1988; Bruinzeel et al. 1997; Tamisier and Dehorter 1999),
3. that they show similar seasonal variations in feeding time, the *wintering strategy*.

On the basis of the results of these analyses we draw conclusions for the management of duck winter quarters in temperate regions.

Methods

Study sites

Data were collected from September 1996 to March 1997 at four protected areas of the Rochefort Marshes, in the department of Charente-Maritime, western France (45°60′ N, 01°00′ W). The study sites varied greatly in structure: at the municipal sewage works of Rochefort (hereafter Stepro) ducks use eight artificial treatment ponds (0.7–9.5 ha, water depth between 1.0 and 1.4 m) and a very shallow (<15 cm depth in most parts) natural pond of 6.5 ha. At the Hunting Reserve of the Cabane de Moins, in Breuil-Magné (hereafter Breuil), ducks use two waterbodies: a deep and large (30 ha) reservoir, with water levels >10 m in some parts, and a shallow pond (maximum depth <50 cm) of 7.5 ha. At the Nature Reserves of Yves and Moëze-Oléron (hereafter Yves and Moëze), ducks concentrate on only one waterbody during daylight hours, of respectively 24 ha at Yves and 32 ha at Moëze. Water depth was <35 and <50 cm in these waterbodies, and water levels generally at all four sites were maintained near constant.

Behavioural observations

Diurnal scan samples of duck behaviour (Altmann 1974) were done between 07:00 and 18:00 h, one day per week at each site, in order to measure average time-budgets. Six to eight scan samples were performed daily at Moëze and Yves. The time necessary to scan several ponds at the Stepro and at Breuil did not allow more than two complete sets of scan samples over the whole site per day, one in the

Table 1. Diurnal and nocturnal numbers of ducks at the four study sites between September 1996 and March 1997 (mean ± SE).

	Mallard		Teal	
	Day	Night	Day	Night
Breuil	272 ± 38 (23)	12 ± 3 (23)	212 ± 23 (23)	21 ± 5 (23)
Moëze	481 ± 68 (19)	40 ± 4 (22)	447 ± 69 (19)	33 ± 5 (22)
Stepro	66 ± 9 (24)	21 ± 4 (23)	148 ± 18 (24)	43 ± 10 (23)
Yves	221 ± 28 (23)	17 ± 10 (23)	144 ± 16 (23)	10 ± 2 (20)

Sample sizes (i.e. number of average weekly values) are indicated in brackets.

morning and one in the afternoon. We distinguished birds which were foraging, moving (i.e. swimming or walking), in comfort activities (resting or preening), vigilant, and involved in social interactions (both sexual and agonistic).

Nocturnal scan samples were also done twice a week at each site, before and after the diurnal observations, except when poor weather prevented visibility (i.e. foggy nights). Diurnal and nocturnal numbers of ducks at each site are presented in Table 1. Nocturnal observations were made using a ×4 binocular light amplifier (Thomson Optronique UGO), at least 2 h before dawn and 2 h after dusk, using the same route across the reserves in each case (Gibbons et al. 1996). Because ducks had to be observed at a closer range at night than during daylight hours, and the observer's presence could have disrupted their nocturnal activities, we considered as foragers all ducks which were active (i.e. either actively foraging, swimming or vigilant), as opposed to birds resting or in comfort activities; this seemed a reasonable assumption since wintering dabbing ducks generally spend most of the night foraging (e.g. McNeil et al. 1992). Nocturnal observations from hides in the reserves showed that the birds did indeed forage for most of the nights. It has been shown that the majority of the ducks using these reserves by day leave them at night (70–90%; Table 1, Guillemain et al. 2002). However, we expect that the observations reported here of the time-budget of the birds remaining in the reserve are representative of the whole populations, since granivorous ducks in other wintering quarters spend most of the night feeding (see above) and casual observations performed from hunting hides showed that ducks also spend most of the night foraging in unprotected feeding areas (N. Guillon and M. Guillemain, personal observation).

The average diurnal foraging activity in the Marshes of Rochefort was compared with data from seven other wintering day-roosts of the Palearctic and the Nearctic in order to test the hypothesis that climatic conditions at a wintering quarter affect the diurnal foraging time of granivorous dabbling ducks (Tamisier 1972a; Paulus 1988; McNeil et al. 1992). Only inland (i.e. not directly in contact with the sea if coastal) wintering quarters were considered, since the distribution of duck foraging time over day and night is known to be affected by tides in littoral areas. One average value over the four sites of the Rochefort Marshes was computed for each species. The average value over the two species was used in the analysis, and the same was done for data from other wintering quarters when several species were studied, so that only one point (the average for the granivorous duck species) was included for

each wintering quarter (this was necessary because duck communities did not always comprise exactly the same species in different wintering quarters). Tamisier's hypothesis (1972a) was that diurnal foraging should be more intense in northern than in southern wintering quarters, because of lower temperatures. Although this should be true within a flyway, climatic conditions at two wintering quarters located at the same latitude in the Palearctic and the Nearctic are very different. We therefore plotted the time spent foraging during daylight hours (expressed in minutes) against both latitude and average January temperature (used as an index of winter climate), which allowed comparison of the effects of these two parameters.

Statistical analyses

The data used in the analyses are average weekly values computed over all scan samples of each study day, separately for nocturnal and diurnal periods. The maximum sample size for each site is the number of weeks of the study period, both for diurnal and nocturnal data. However, the data from days with exceptionally poor weather (i.e. fog that prevented observations and frozen conditions) were discarded from the analyses, which reduced the sample size and caused differences in the number of data between sites, and between day and night. Sample sizes also differ between mallard and teal at some sites, because one of the species was occasionally absent. Behavioural data are presented as percentages throughout the paper, but analyses were performed on proportions when using non-parametric tests, or with arcsine-transformed proportions for parametric ones (Sokal and Rohlf 1995).

The total foraging time per 24 h (hereafter daily foraging time) was computed using diurnal and nocturnal proportions of time spent foraging, and the hours of sunrise and sunset from the national postal service almanac, considering that night started 1 h after sunset and ended 1 h before sunrise. The average length of the nights was calculated for each month of the winter. Nocturnal and diurnal data were not always available for each study day because of poor weather, leading the sample size for daily foraging time to be smaller than either the diurnal or the nocturnal sample sizes. As the length of the nights was calculated on a monthly basis, we calculated an average monthly proportion of diurnal time spent foraging for each species at each site, which was used to assess if ducks adjust the distribution of feeding time between night and day when the length of nights varies (Owen 1991; McNeil et al. 1992; Tamisier and Dehorter 1999).

It is possible that the same birds were observed during two successive weeks. Given the relatively large numbers of individuals observed at each site each week, this is very unlikely to have important consequences for our estimates of the proportion of time spent foraging and daily foraging time (which might otherwise have been biased if very small numbers of individuals with a particular behaviour were repeatedly sampled). However, in order to take into account potential auto-correlation between values for successive weeks, we used SAS MIXED procedures (SAS Institute 1990) with week number for which data were available included as a random effect: the significance of independent factors was assessed given the

potential role of 'week'. Analyses included comparisons of the proportion of diurnal or nocturnal time spent foraging between species and sites, and comparisons of daily foraging times between species, sites and periods of the winter, i.e. early, mid- and late winter (September–October, November–December and January–15 March, respectively).

Results

Diurnal foraging in protected areas

Over the four sites at Rochefort, foraging represented 9.7% (± 4.3 SE, $n = 4$) of the diurnal activities of mallard, and 22.9% (± 5.9 SE, $n = 4$) of the diurnal activities of teal. The average value for granivores of Rochefort (i.e. 16.3%, or 101 min) lies within a gradient of decreasing diurnal foraging time with increasing average January temperature at a given wintering quarter (Spearman rank correlation: $r_s = -0.94$, $df = 6$, $P = 0.0005$; Figure 1). The relationship between diurnal foraging time and latitude was also significant ($r_s = 0.73$, $df = 6$, $P = 0.0366$).

The proportion of diurnal time spent foraging differed between mallard and teal and between sites, with no significant effect of the interaction 'Species × Site' ($F_{3,170} = 1.62$, $P = 0.1865$). When the interaction was removed from the analysis, both 'Species' and 'Site' remained significant (Table 2): mallard spent more time foraging during daylight hours than teal, and Bonferroni-adjusted t-tests ran per species showed that both mallard and teal fed more during daylight hours at the Stepro site than at the other sites (P values all <0.0130; Figure 2). The percentage

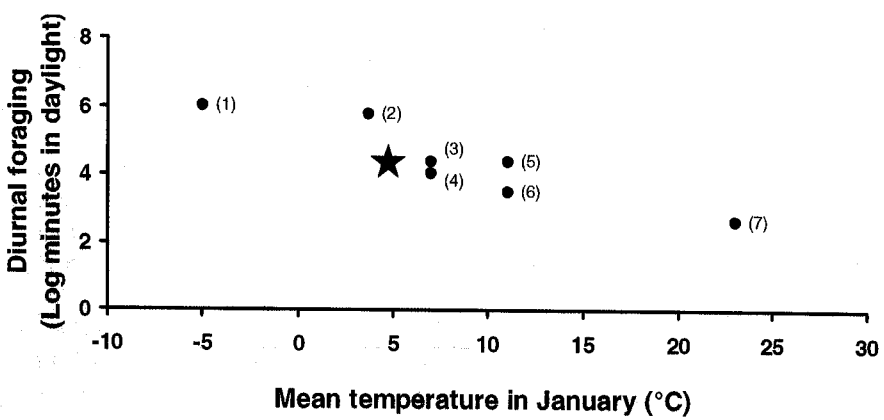

Figure 1. The relationship between the temperature and the diurnal time ducks spend foraging in different wintering quarters: foraging time decreased with increasing temperature (see text for statistics). Data from this study are indicated by a star. Numbers in brackets: (1) Jorde et al. (1983) [Nebraska], (2) Thomas (1982) [Ouse Washes, England], (3) Quinlan and Baldassarre (1984) [Texas], (4) Miller (1985) [California], (5) Tamisier (1972b) [Camargue, France], (6) Tamisier (1976) [Louisiana], (7) Roux et al. (1978) [Senegal].

Table 2. Results of a MIXED procedure of the proportion[a] of diurnal time spent foraging by wintering ducks with 'Site' and 'Species' as factors (n = 180 observations).

Source	*df*	*F*	*P*
Species	1	31.47	<0.0001
Site	3	19.60	<0.0001

[a]Arcsine-transformed data were used in the analysis.

of diurnal time spent foraging did not correlate significantly with the length of nights for any species at any site (Spearman correlations over average monthly values, all $P > 0.05$, n = 7 months in all cases).

Nocturnal foraging in protected areas

Most of the night was spent foraging by mallard and teal at the four study sites (i.e. 79.9% ± 7.5 SE and 90.7 ± 2.2 SE, respectively, n = 4 sites in both cases). 'Species', 'Site' and the interaction 'Species × Site' had a significant effect on the proportion of nocturnal time spent foraging (Table 3): differences between species were not consistent across sites. Bonferroni-adjusted t-tests showed that mallard fed less than teal at the Stepro and Yves sites, which were also the two sites where mallard fed less during the night (P values all <0.05; Figure 3). No significant difference was observed between sites for teal. We did not find any significant correlation between the percentage of diurnal time spent foraging and the percentage of nocturnal time spent foraging (Spearman correlations, all $P > 0.05$).

Daily foraging time of the two species

Only 'Species' had a significant effect on the daily foraging time ($F_{1,132} = 22.63$, $P < 0.0001$), while no significant effects of 'Site' and 'Site × Species' were observed,

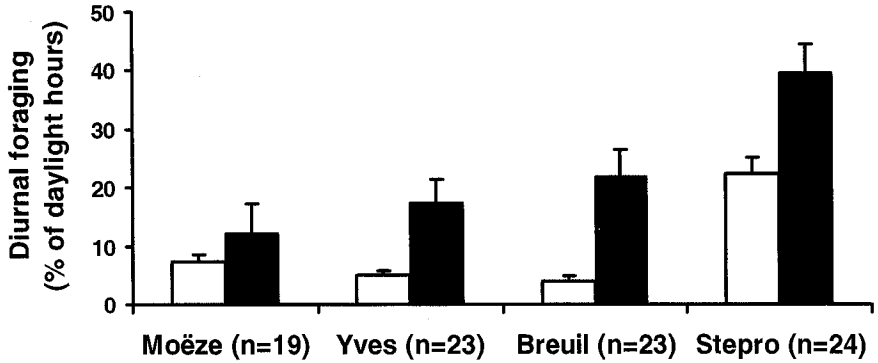

Figure 2. Diurnal foraging time by mallard (white columns) and teal (black columns) at the four study sites. Columns are means, vertical bars show standard errors. Sample sizes (i.e. number of average weekly values) are indicated in brackets for each site. Both species spent more time foraging at the Stepro site than at the other sites, while teal always foraged longer than mallard (see text).

Table 3. Results of a MIXED procedure of the proportion[a] of nocturnal time spent foraging by wintering ducks with 'Site', 'Species' and the interaction 'Species × Site' as factors (n = 143 observations).

Source	df	F	P
Species	1	9.48	0.0025
Site	3	5.31	0.0017
Species × Site	3	3.96	0.0097

[a]Arcsine-transformed data were used in the analysis.

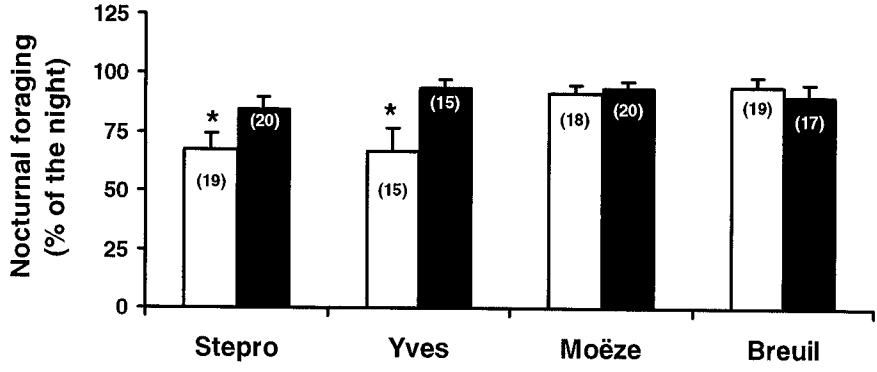

Figure 3. Nocturnal foraging time by mallard (white columns) and teal (black columns) at the four study sites. Columns are means, vertical bars show standard errors, and sample sizes (i.e. number of average weekly values) are indicated in brackets for each species and site. Stars indicate significantly different foraging times (see text).

Table 4. Results of a MIXED procedure of the daily foraging time of dabbling ducks with 'Species', 'Period' and the interaction 'Species × Period' as factors (n = 135 observations).

Source	df	F	P
Period	2	3.71	0.0272
Species	1	23.67	<0.0001
Period × Species	2	9.89	<0.0001

and these factors were therefore removed from the analysis: the daily foraging time was longer for teal (13 h 39 ± 14 min SE per day, n = 4 sites) than for mallard (10 h 48 ± 43 min SE per day, n = 4 sites) across sites.

When daily foraging times were also compared between periods of the winter, adding 'Period' and 'Species × Period' to the comparison between species in the analyses, the three factors were significant (Table 4): the difference between species was not constant throughout the winter. Shorter daily foraging times for mallard in early winter were responsible for this pattern: Bonferroni-adjusted t-tests between all species and periods only revealed differences between early winter and mid- or late winter in mallard (both $P < 0.0075$), and between early winter mallard values and teal values for the three periods (all $P < 0.0013$; Figure 4). When data from early winter were excluded from the analyses, the significant difference previously observed between the daily foraging times of mallard and teal disappeared ($F_{1,82}$ =

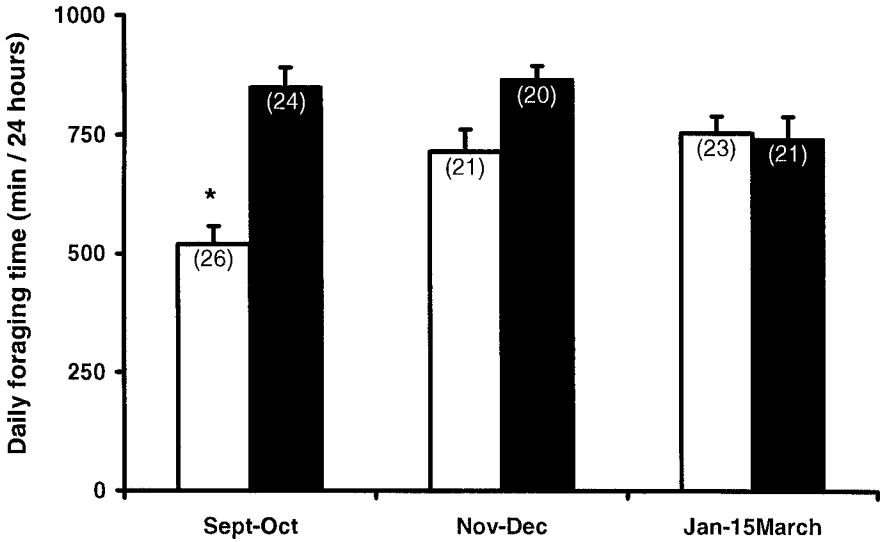

Figure 4. Daily foraging time of mallard and teal in the Marshes of Rochefort during early, mid- and late winter (September–October, November–December and January–15 March, respectively). Columns are means (in minutes per 24 h), vertical bars show standard errors. Sample sizes (i.e. number of average weekly values) are indicated in brackets for each case. The daily foraging time of mallard was lower in early winter than in the two other periods (see text).

2.79, $P = 0.0989$): the early winter values were therefore the source of the differences between species in daily foraging time across winter.

Discussion

Diurnal foraging at the holarctic scale

Wintering granivorous ducks spend most of the night foraging (Roux et al. 1978; Thomas 1982; Jorde et al. 1983; Quinlan and Baldassarre 1984; Miller 1985; McNeil et al. 1992), and the data of Tamisier and Dehorter (1999), who reported that teal in the Camargue spent 84% of the night foraging, are consistent with our results for teal and mallard in Rochefort (80 and 90%, respectively). Teal fed for 12–40% of daylight hours in the protected areas of the Marshes of Rochefort, mallard for 4–22%. Overall, with the four sites weighted equally, these two species fed for 16% of the daylight hours. These results, and those from other studies, show a sharp gradient of increasing diurnal foraging time with decreasing average temperature in January across a variety of wintering sites, and provide the first evidence that climatic conditions at a wintering quarter are a major determinant of dabbling duck time-budgets (Tamisier 1972b; Paulus 1988; McNeil et al. 1992). The relationship between foraging times and latitude is barely significant, and though the two correlation coefficients are not significantly different we suggest that

temperature rather than latitude should be considered when comparing feeding behaviour between wintering quarters at the holarctic scale. We therefore accept hypothesis 1 and broaden the conclusions to a wider geographic scale. Other factors such as hunting, predation pressure and site suitability for foraging may also affect the day–night distribution of foraging time by dabbling ducks, or even their daily foraging time overall. Although these factors will have to be accounted for in the future, no data are available at present to carry out a broader analysis of all the factors that may affect duck foraging times at a very large scale.

From a conservation point of view, this relationship between time-budgets and climatic conditions suggests that the provision of good diurnal foraging conditions for ducks may improve their survival in cold wintering quarters, but not in milder areas. Diurnal foraging habitats have been created experimentally around Lacassine Pool in Louisiana (mini-refuges; Cox and Afton 1998), and are seldom used by Pintail (*Anas acuta*) during daylight hours (Cox and Afton 1998, 1999). This is in agreement with the pattern in Figure 1 as the climate of Louisiana in winter is mild, so it is likely that ducks have low energy requirements, which they are able to fulfil during the night.

Interspecific differences

In the protected areas of the Marshes of Rochefort, over the winter teal foraged longer per day than mallard, which was consistent with the results of Bruinzeel et al. (1997), showing that smaller Anatidae have longer foraging times because they have more difficulty in balancing their daily energy requirements. In agreement with the results above, longer daily feeding times in teal resulted from this species foraging twice as much as mallard during the daylight hours: nocturnal foraging times were more often similar. The difference we observed between teal and mallard seems to be a consequence of different migration strategies rather than a consequence of contrasted body masses *per se*, since the daily foraging time was not significantly different between species when data from early winter were excluded from the analysis. Early winter (September–October) was the period when the daily foraging time of mallard was the shortest. Mallard seldom migrate in western France (Rüger et al. 1987; Monval and Pirot 1989), and consequently do not have to refuel their reserves after migration. Further, food resources for granivorous ducks are likely to be most abundant in early winter in western France (e.g. Guillemain et al. 2000c). We therefore reject the second hypothesis.

The wintering strategy pattern proposed by Tamisier et al. (1995) predicts that the daily foraging time of ducks should decrease in mid-winter. We did not observe this in either species. The daily foraging time of granivorous dabbling ducks seems to be driven by climatic conditions at the wintering quarter, and western France is colder than the Camargue. It is therefore likely that it is more difficult for the birds in western France to build their reserves and maintain them in mid-winter, so in our study area they feed longer in November and December. We therefore reject the third hypothesis.

Day–night distribution of feeding time

We did not find any significant relationship between the percentage of time spent foraging during daylight hours and the length of nights or the nocturnal feeding time the same day for these granivorous ducks. This differs from the results obtained for shoveler at the Stepro site, where these birds increased their diurnal foraging time in response to exceptional poor nocturnal foraging conditions (i.e. wind that made planktonic prey less available; Guillemain et al. 2000b). The nocturnal foraging activity of mallard and teal showed little variations, which was not surprising since the weather does not affect seed accessibility to the same extent as it affects zooplankton availability.

The percentage of the daytime spent foraging did not increase with decreasing length of nights either, though this occurs elsewhere (see review in McNeil et al. 1992). This could be due to the fact that we used average monthly values, and these were not precise enough, as the length of the night shows strong variations within winter months.

Differences between sites in the Marshes of Rochefort

The daily foraging time of teal and mallard did not differ significantly between sites in the Marshes of Rochefort, but the distribution of foraging activities between day and night differed among the four sites, with longer diurnal feeding times at the Stepro site. A previous study showed that the number of resident marsh harrier (*Circus aeruginosus*), a potential predator of dabbling ducks, was lower at the Stepro site than at Moëze and Breuil (Fritz et al. 2000). This, associated with the fact that Stepro is the only site with a very shallow (<15 cm deep) pond, might explain the higher foraging activity of ducks at this site: in addition to potentially lower predation risk, ducks were able to forage in most parts of the pond with only their bill submerged, a method associated with higher food intake rates (Guillemain et al. 2000a) and shorter vigilance time (Guillemain et al. 2001) than when upending.

In summary, this paper supports the hypothesis that climatic conditions at the wintering quarters of dabbling ducks, which affect their energy requirements, are a major factor determining their foraging activity in protected areas during this season. The two species we studied are close to the extreme body masses of dabbling ducks, but had similar, very long feeding times except in early winter, where feeding time seemed to depend upon migratory strategies. The migratory status of species that use a given site should thus also be taken into account in the management of that site. Most sites where ducks concentrate during daylight hours in Africa and western Eurasia are now protected, at least to some extent (Scott 1980; Scott and Rose 1996). Managers of sites located in colder areas may wish to take into account the fact that some ducks may be energetically stressed, and have to find suitable foraging conditions at sites they use during daylight hours, and adjust the management of the sites accordingly.

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