

Foraging methods can affect patch choice: an experimental study in Mallard (*Anas platyrhynchos*)

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Abstract

Animals can adapt to changes in feeding conditions by switching between foraging methods. Dabbling ducks use different foraging methods, including dabbling in deep water with the head and neck submerged, and grubbing in the mud (or shallow water) where the eyes are above the surface, so the bird can visually monitor its environment while foraging. Deep foraging is considered to provide lower intake rates and to have high associated costs, such as predation risk, compared to shallow foraging. Ducks should thus prefer shallow foraging and switch to deeper methods when feeding conditions deteriorate. We conducted a set of experiments with Mallard to assess the importance of intake rate as a cue to choose between patches associated with different foraging methods, and evaluate the influence of food depletion on the decision to switch between methods. When 50 g of wheat were presented in two patches, one at a depth of 5 cm and one at 35 cm, most of the foraging was in the shallow area. Reducing food abundance to 10 g in the shallow area led to an increase in deep foraging, although the birds still preferred the shallow area at the beginning of the tests despite the fact that it did not provide a higher intake rate. This area was used until complete depletion, and birds did not turn to deep foraging before ensuring that the shallow patch was empty. These results show that food depletion affects the choice between feeding patches hence foraging method. However the value of intake rate is not the main cue for decision, rather the birds appear to choose between patches with different methods on account of their respective costs. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Foraging behaviour; Patch choice; Laboratory experiments; Mallard; Food intake rate

1. Introduction

Animals cope with changes in spatial and temporal variations in the abundance of their food resources in a variety of different ways: switching

between habitats, patches or diets have received much attention (e.g. Stephens and Krebs, 1986; Brown, 1988; Brown and Mitchell, 1989; Hughes, 1993, Sutherland, 1996). Conversely, switching between foraging methods has been much less studied, except for the case of predators turning from ambush (sit-and-wait) to active search of prey (Grant and Noakes, 1987; Village, 1990; Fausch et al., 1997). The switch between methods is in

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this case often linked to a switch between prey types (e.g. Nakano et al., 1999). Switching between methods can also lengthen patch residence time, by allowing a more complete use of the feeding area without any diet shift (Pöysä, 1989). Switching between methods can also occur when animals use different food patches, whose physical characteristics constrain the behaviour of foragers. In this case, the costs of each method should be taken into account by foragers while switching from a patch to another.

While studying granivorous dabbling ducks wintering in the marshes of Western France, we observed that they progressively changed their foraging methods during the course of winter (Guillemain and Fritz, unpublished MS). Ducks use a wide range of methods, and show great flexibility in their foraging behaviour (e.g. Thomas, 1982). Still, the feeding methods can be classified into two basic categories: (1) dabbling in deep water, where the eyes are underwater; and (2) grubbing in mud or shallow water with the eyes above the surface (hereafter deep and shallow foraging, respectively). These methods are thought to be associated with different intake rates, predation risks, and energy demands (Pöysä, 1987), which should lead to a clear hierarchy in the preferences shown for these foraging methods, and therefore for feeding patches associated with them.

Our field data show that ducks fed in deeper water as winter progressed, in relation to the increasing cumulative number of foragers at the site, which suggests that shallow foraging was the preferred method. We have shown in experimental tests that shallow foraging provides higher intake rates.

The goal of the present study was, first, to assess experimentally if the depletion of food resources does lead ducks to change their foraging methods. We thus tested the preference between shallow and deep foraging with equal food densities, expecting that the shallow patch should be selected first. We then simulated food depletion by offering a lower food density in the shallow area, expecting that ducks would turn to deep foraging. Finally, we study the decision rules as-

sociated with switching between foraging methods, by testing if the proportion of time spent in each method reflects differences in food intake rates, and to what extent birds take the costs of the different feeding methods into account.

2. Methods

Experiments were carried out during spring and summer 1999 at the Centre d'Etudes Biologiques de Chizé, in western France, on nine captive Mallards from third generation birds caught in the wild. The ducks were kept in a 15 m² enclosure for the experiment periods; they had access to a 400 m² fenced area between tests. The enclosure comprised a 2 m² tank, with adaptable trays that allowed us to adjust water depth independently in the two halves. Because granivorous dabbling ducks, including Mallard, search for food in the sediment of water bodies from the surface of the water, each feeding patch was necessarily associated with a unique foraging method, determined by the water depth. One half of the tank was adjusted to a depth of 5 cm, and one to 35 cm. Depths were defined so as to limit duck foraging behaviour to one of two postures: grubbing and upending (i.e. feeding with only the bill underwater in shallow water, and feeding with the whole anterior part of the body submerged in deep water, respectively, *sensu* Thomas, 1982). The depths were switched between sides in successive tests to avoid confounding side and depth effects. Birds could enter and leave the tank freely during the experiments. The food, wheat grains, was covered by a thick layer of fine sand to avoid visual detection. Ducks were fed *ad libitum* with wheat and poultry pellets between tests, and were deprived of food for the night before the experiments. Small groups of birds (one male and two females randomly assigned to the different groups for each test) were used, as ducks used in isolation did not show normal feeding behaviour in the experimental tank. No bird was involved in more than one test per day. Three different experiments were carried out.

2.1. Experiment 1

The goal of this experiment was to test the hypothesis that Mallards prefer shallow foraging when equal food densities are given at different depths and travel costs between patches are negligible. Fifty grams of wheat were provided both at 5 cm (shallow area), and 35 cm (deep area).

2.2. Experiment 2

The goal of this experiment was to test the hypothesis that food depletion in the shallow area induced a switch to deep foraging. In order to simulate food depletion, the same procedure was followed, but at 5 cm only 10 g of wheat were offered.

Ten replicates of experiments 1 and 2 were performed. Amounts of wheat left in the two patches were weighted at the end of each trial. In both experiments, the behaviour of the three ducks was recorded at the end of every 5 min periods for 3 h (scan sampling, Altmann, 1974). The last 5-min period was not included in the analyses, because we had to enter the experimental area to prevent ducks from foraging for longer than 3 h, which reduces the number of time intervals to 35 in both experiments 1 and 2. We distinguished shallow foraging, deep foraging and non-foraging activities. In order to test for a preference for either shallow or deep foraging, we first compared the distribution of foraging behaviour records at the two depths (i.e. number of times a bird was observed to forage in one patch) with a random distribution by chi-square tests, pooling data from all individuals in all trials. This was made separately for experiments 1 and 2. In order to assess if an artificial decrease of food abundance in the shallow area lead to a higher use of the deep patch, we then compared the distributions of foraging behaviour records in the two patches during experiments 1 and 2, still with a chi-square test.

We then assessed how the use of the deep patch varied across time in each experiment. The probability of a forager to use the deep patch across time in experiments 1 and 2 was studied using a logistic regression including time (i.e. observation

intervals), experiment (1 or 2) and the interaction time \times experiment as explanatory variables. Maximum-likelihood estimates (\pm S.E.) and the results of the maximum-likelihood analysis-of-variance (i.e. chi-square values) are presented for each explanatory variables. A significant chi-square value for a given parameter in the maximum-likelihood analysis-of-variance indicates that including this parameter significantly contributes to the fit of predicted values to observed data.

2.3. Experiment 3

This experiment was performed in order to assess the relationship between patch choice and food intake rate in the first part of the tests. We used the same experimental set-up than during experiment 2, i.e. 10 g of wheat in the shallow patch and 50 g of wheat in the deep patch, but the tests were interrupted after 5, 10 or 15 min. We weighted the amount of wheat left at 5 and 35 cm at the end of the trials, of which five were performed for each test duration. Experiments were video-taped, which allowed the behaviour of individuals to be monitored constantly (focal individual sampling, Altmann, 1974). This allowed us to measure the time spent feeding at each depth by the three ducks during in each trial, which were subsequently divided by three to compute a mean individual feeding time per patch per trial. In order to study patch choice by Mallards, we used Wilcoxon paired-tests to compare average individual feeding times at each depth over five replicates, for the three test lengths.

Upending forces ducks to interrupt their feeding regularly (Pöysä, 1987), thus the foraging time is made of feeding bouts plus interruptions between bouts for birds that use the deep patch. The birds also performed non-feeding activities, such as preening or interacting with each other: in these circumstances the interruptions were longer. We defined as interruptions between 'meals' those which were longer than the median inter-bout length plus the standard error for each individual duck. Inter-bout interruptions were never > 7 s in any individual, due to the highly skewed Poisson distribution of feeding interruptions. Foraging time thus refer to upending bouts plus 'short'

interruptions, while ‘long’ interruptions were discarded. Estimations of the instantaneous intake rate per group of three birds (in grams ingested per minute foraging) were calculated for each trial, in each set of test duration, by the ratio of the amount of wheat consumed on the foraging time, and subsequently divided by three to obtain an estimation of the average instantaneous intake per individual in each trial. This was made separately for the deep and the shallow patches, whose values were compared by Wilcoxon paired tests. In some trials (i.e. one trial for 5 and 10 min tests, 2 trials for 15 min tests) birds did not use the deep patch, which prevented us to measure instantaneous intake rates. Despite five trials were performed for each test length, Wilcoxon tests of food intake rates thus refer to three or four paired values.

3. Results

When 50 g of wheat were presented at both depths (experiment 1), 112 of 143 foraging behaviour records took place in the shallow area, which was significantly different from a random distribution ($\chi^2 = 45.88$, $df = 1$, $P < 0.001$). An opposite preference was observed when food den-

sity was reduced from 50 to 10 g in the shallow area: in experiment 2, the distribution of foraging behaviour records also differed significantly from random ($\chi^2 = 12.20$, $df = 1$, $P < 0.001$), and 114 of 181 events took place in the deep patch. A lower food abundance in the shallow area thus affected significantly the distribution of foragers over shallow and deep patches ($\chi^2 = 55.12$, $df = 1$, $P < 0.001$).

Proportions of deep foragers across time in experiments 1 and 2 are shown in Fig. 1. The maximum-likelihood analysis-of-variance revealed that both ‘time’ and ‘experiment’ significantly contributed to the fit of predicted values to observed data (chi-square tests of goodness of fit, respectively: $\chi^2 = 22.34$, $df = 1$, $P < 0.0001$ and $\chi^2 = 19.58$, $df = 1$, $P < 0.0001$). Maximum-likelihood estimates of the logistic regression were positive for both ‘time’ (i.e. 0.011 ± 0.002 S.E.) and ‘experiment’ (i.e. 1.088 ± 0.246 S.E.), suggesting that the probability of a forager to select the deep area increased across time and differed between experiments 1 and 2. The maximum-likelihood estimate for ‘time # experiment’ was negative (i.e. -0.001 ± 0.002 S.E.), but including this parameter into the analysis did not improve the fit of predicted values to observed data ($\chi^2 = 0.04$, $df = 1$, $P = 0.8440$), suggesting that the

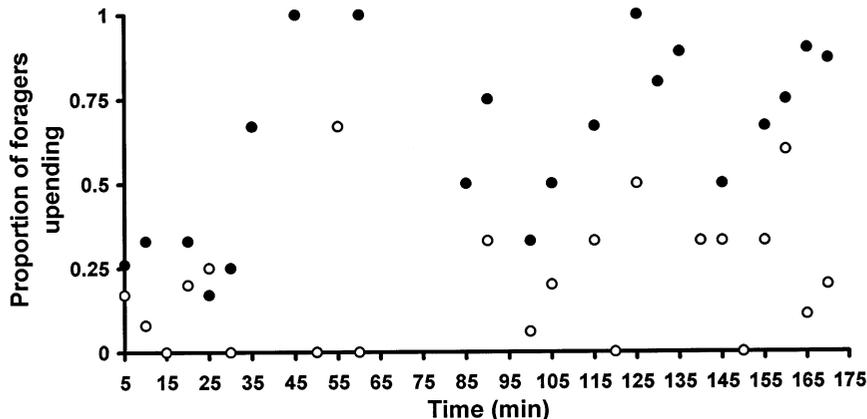


Fig. 1. Proportion of foragers upending when food availability was 50 g both in the shallow and deep areas (white circles, experiment 1), and when food availability was reduced to 10 g in the shallow patch and still at 50 g in the deep area (black circles, experiment 2). Observations were performed at the end of 5 min intervals, except the last one, for 3 h. Note that to avoid inflating the sample size, scan samples where no ducks were foraging were not included. Consequently, points are missing for some of the time intervals.

Table 1

Individual feeding times in shallow and deep patches for the three test durations of experiment 3^a

Test duration (min)	Feeding time in the shallow patch (5 cm)	Feeding time in the deep patch (35 cm)	Wilcoxon paired test	
			Z	P
5	31.65 ± 4.14	4.24 ± 2.00	-2.023	0.043
10	56.03 ± 5.79	7.11 ± 3.12	-2.023	0.043
15	89.58 ± 27.51	29.37 ± 25.34	-2.023	0.043

^a Values are expressed in seconds (mean ± S.E.), averaged over five trials per test duration. Note that Z and P values of Wilcoxon paired tests are the same for the three test durations because for all the trials of all test durations the feeding time in the shallow patch was always higher than the associated feeding time in the deep patch.

probability of a forager to select the deep area did not increase with time at a different rate between experiments. At the end of experiment 2, all the food (10 g) available at 5 cm had been consumed in all ten tests, while at 35 cm the three ducks consumed 34.1 g on average (± 2.4 S.E., $n = 10$) per trial.

In experiment 2, Mallards used the deep area more heavily than during experiment 1 but, however, the shallow area was still used for a long time: in the last hour of experiment 2, 15.7% (± 6.6 S.E., $n = 10$) of foraging ducks were using the shallow patch. Ducks were free to move in and out of the feeding tank during the experiments. When the ducks entered the patch after they left it temporarily, they generally searched the shallow area before turning to deeper foraging ($n = 25$ of 34 entries: significantly more than 50%, $\chi^2 = 7.53$, $df = 1$, $P < 0.01$).

Experiment 3 shows that, even when food density was five times less in the shallow than the deep area at the beginning of the tests, birds spent more time feeding in the shallow patch during the three test lengths: 5, 10 and 15 min (Table 1). This preference, despite the fact that instantaneous intake rates did not differ between depths (Fig. 2) suggests that there are costs involved in foraging in deep water. Food depletion occurred at 5 cm, where after 15 min the patch was completely empty in three of five trials, and 0.2 g remained after the two other ones. At 35 cm, conversely, ducks consumed few amounts of wheat, even no wheat at all in two of the five trials (Fig. 3). The fact that ducks still searched the shallow area in

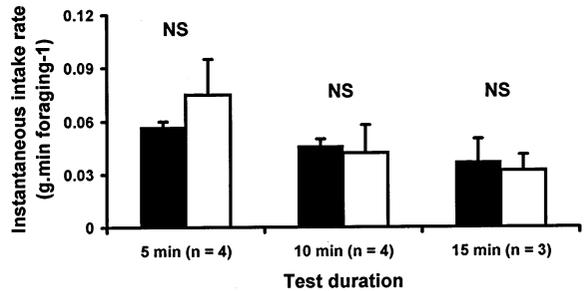


Fig. 2. Individual instantaneous intake rate of Mallards during 5-, 10- and 15-min tests. Columns are means \pm S.E. Black columns refer to the shallow area (5 cm), white columns to the deep area (35 cm). Sample sizes (number of groups of three ducks for which both shallow and deep values were available) are indicated on the X-axis. Values were compared between the depths for each test duration by Wilcoxon paired tests, which provided significant results in no case (all $Z < 0.730$, all $P > 0.46$).

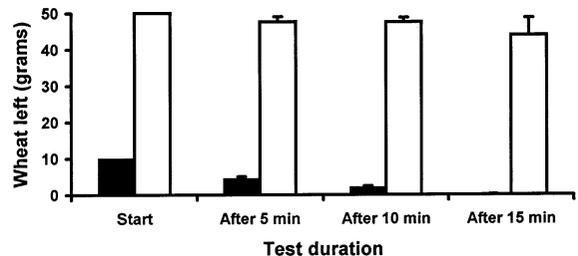


Fig. 3. Amounts of wheat provided at the beginning of experiment 3 and left after 5-, 10- and 15-min tests. Columns are means \pm S.E. Black columns refer to the shallow area (5 cm), white columns to the deep area (35 cm). Sample sizes (number of groups of three ducks) are $n = 5$ in all cases.

the last hour of experiment 2 (when food was completely exhausted there) thus suggests that the birds ensured that the shallow patch was completely empty before turning to deep foraging.

4. Discussion

When food was equally abundant at 5 and 35 cm, Mallards showed a strong preference for foraging in the shallow part of the tank (experiment 1). In experiment 2, a reduction of food density in the shallow patch led the Mallards to turning to deep foraging, which supports the hypothesis that food depletion is responsible for the switch from shallow to deep foraging observed in dabbling ducks in the wild. When food availability in the shallow area was reduced to 10 g m^{-2} , the food intake rate in shallow water fell to the same level as that from deep foraging, but the Mallards nevertheless continued to select the shallow patch during the first 15 min of the tests. This suggests that deep foraging has costs that ducks incorporate into their decision rules. Numerous studies have shown that the risk of predation is one of these costs that affects decision rules of foragers (e.g. Milinski and Heller, 1978; Werner et al., 1983; Lima, 1985; Kotler, 1997). Deep foraging is assumed to increase the vulnerability of ducks to predation: the main response of these birds when a predator appears is a prompt take-off by all individuals (Tamisier and Dehorter, 1999), and deep foragers with eyes underwater cannot detect danger immediately. Pöysä (1987) showed that the probability of detecting an approaching predator with an attack time of 1 s was reduced by almost 60% for a solitary upending teal in comparison with a solitary grubbing individual. In addition, the particular structure of the feeding sessions during upending leads to a loss of effective foraging time through a reduction of the time spent straining food during the feeding sessions (Pöysä, 1987). Previous experiments where ducks were restricted to only one foraging method showed that grubbing Mallards had long feeding bouts at a low frequency (i.e. 22.3 s , 2.6 min^{-1}), while upending ducks had short and frequent feeding bouts (i.e. 2.3 s , 12.2 min^{-1}) and an average

transit time of 0.4 s from the beginning of the bill immersion to the vertical extended upending posture (unpublished data). Mallard feeding at 5 cm can thus spend 97% of their foraging time actively straining food, while this value would be as low as 39% for upending birds. This 60% reduction of the effective feeding time must represent an important cost, as the ducks must increase their daily foraging time considerably.

Scan sampling of flock behaviour gives the proportion of individuals in each behaviour category, which can be used as an estimation of the average proportion of time each individual spends in that behaviour (Altmann, 1974). Scan sampling data allowed us to calculate individual feeding time between the 15th min and the end of experiment 2. These calculations, combined with intake rate values of experiment 3, suggest that if Mallards spent their whole feeding time in the deep area rather than searching the shallow part of the tank when it was depleted (i.e. after the 15th min), each bird would have had ingested 14.04 g until the end of the trial (considering intake rate as being constant over time, similar to that of the 15 min tests of experiment 3). By contrast, differences between the amounts of wheat left at the end of experiment 2 and at the end of the 15 min tests of experiment 3 suggest that each duck actually ate 9.35 g at 35 cm between 15 min and 3 h, thus 4.69 g of wheat less, or a 33.40% lower food intake. This suggests that rewards expected from shallow foraging are sufficiently higher than those from deep foraging for the ducks to accept an important reduction of their intake by searching the shallow patch systematically before turning to the deep area.

It is possible that the birds showed this pattern of behaviour because in captivity they were sure to be fed between tests, and could consequently afford to abandon optimality considerations and spend a long time exploring sub-optimal patches. The fact that this study was conducted on captive birds which could predict that they would be fed between tests could explain the moderate interest they devoted to feeding during experimental tests (in experiments 1 and 2, foraging represented 14 and 17% of the total time-budget, respectively; see the number of missing values in Fig. 1). However,

if birds abandoned any optimality considerations some of them should have used the deeper patch for the length of the test in the first experiment, which was never observed.

This study describes the ability that animals have to switch between foraging methods in some circumstances, an aspect of foraging behaviour that has received little attention (Stephens and Krebs, 1986). Our results show that the use of shallow and deep foraging by Mallards did not match the ratio of intake rate values from distinct methods, which suggests that when different patches need different foraging methods, costs may exist when switching from a method to another. In the context of optimal foraging theory, considering that foragers can change their methods and incorporate the costs associated with each of them into their decision rules has important consequences for our understanding and the modelling of foraging patch choice.

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