Interruptions of terrestrial feeding as a way to decrease the non-digestible fraction of the bolus: field observations and laboratory experiments in Mallard.

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Dabbling ducks commonly feed on land, especially in agricultural environments. During field observations in western France, wintering Mallards Anas platyrhynchos were observed to interrupt terrestrial feeding regularly and go to the water. Laboratory experiments show that feeding interruptions occur when food is mixed with non-digestible material, and that water is used to filter this indigestible bulk. When filtering is impossible because of water deprivation, the ingestion of non-digestible material reduces the 24 hour intake of wheat in the laboratory. Terrestrial feeding interruptions have important costs, feeding sessions increased in length when ducks fed farther from water. Since the birds need water, and interruptions have a cost, only a fringe of vegetation around the water-bodies is used by terrestrial foraging Mallards.

These results clarify our understanding of the cause of this behaviour in Mallards, and may have implication for the design of nature reserves.

Key words: *Anas platyrhynchos*, Food intake, Foraging tactic, Experiments.

Among *Anatidae*, *Anas* species generally feed on submerged food while swimming, hence the term "Dabbling ducks". The species of this genus use a wide range of food resources during winter, with some species being either carnivorous (Shoveler *A. clypeata*), herbivorous (Wigeon *A. penelope* and Gadwall *A. strepera*), or granivorous Teal (*A. crecca*), Pintail (*A. acuta*) and Mallard (*A. platyrhynchos*) (Thomas 1982).

Terrestrial feeding can become the main foraging behaviour of dabbling ducks in some conditions, as shown by the intensive use of harvested cereal or potato fields by waterfowl during both the winter (Thomas 1981; Jorde *et al.* 1983; Baldassarre & Bolen 1984) and the breeding season (eg Krapu 1974). A previous study showed that dabbling ducks should select seeds rather than foliage in such conditions, because it would take too long for birds to meet their daily energetic requirements on the second type of food (Bruinzeel *et al.* 1997).

In natural environments, two sources of food are available to granivorous species: seeds in the water (at the bottom of the water column or accumulated by wind on the shore; see Thomas 1982) and seeds on dry land. Underwater foraging has associated costs (*eg* increased predation risk, reduced intake rate; Pöysä 1987, 1989). Terrestrial feeding is adopted by many individuals whenever habitat characteristics make it possible, *ie* when benefits are greater than those from underwater foraging. During winter surveys of wildfowl, we found that more than 20% of foraging Mallards were feeding on dry land in some wintering sites of western France (unpub. data). Observations at close range showed that birds were digging in the substrate to collect food items. Since invertebrates densities in upper layers of the substrate are very low during winter, and no part of vegetative material was sticking out the bill of Mallard, it was unlikely that birds were foraging on animal prey or subterranean parts of plants. Rather, the typical granivorous diet of Mallard in winter suggests that birds were collecting natural seeds (no waste grain was available) in the first centimetres of the sediment in the same way that they forage at the bottom of waterbodies.

These terrestrial foraging birds interrupted feeding several times per minute, walked to the shore, and then returned to their initial foraging spot, which resembled the behavioural pattern described by Thomas (1981) for this species foraging in potato fields. This foraging tactic seemed very costly, and birds should adjust their behaviour to variations in the cost of interruptions. These costs are likely to increase with the distance between the water and the feeding patch.

The first aim of this paper is to determine by laboratory experiments how water is used during the feeding process. Two hypotheses are tested :

■ Water could be necessary to swallow the bolus contained in the bill (Duke 1986a). In this case, Mallards would store food in their bills, ingesting it only when water was present.

■ Alternatively, water could be needed to wash the excess of non-digestible material mixed with the food, by a filtering process through the lamellae of the mandibles (Thomas 1982, Crome 1985, Kooloos & Zweers 1991). In this case, birds would alternate feeding and visits at the water when possible, although ingestion would be possible without access to water. In this later case, the intake rate should be lower when non-digestible material can not be washed out.

The second aim of this paper is to assess if Mallards adjust the length of terrestrial feeding sessions in response to increasing cost of interruptions when feeding farther from water. The behaviour of Mallards was studied at two sites during the winters 1995-96 and 1996-97 to compare the behaviour of ducks in contrasted habitats with different duck numbers, in order to observe how they adapted their terrestrial feeding to varying foraging conditions.

Methods

Laboratory experiments

Laboratory experiments were carried out at the *Centre d'Etudes Biologiques de Chizé* (western France) in January and February 1997 on captive Mallards born in 1996 at the CEBC. Birds were kept in a yard of 200 m^2 where they could freely move between an area (100 m^2) of small shelters protected from aerial predation by a net, and 100 m^2 of grass with a 25 m^2 pond.

The first experiment was carried out to measure the frequency of feeding interruptions with different feeding constraints: we kept 21 ducks together in a 30 m^2 enclosure for the length of the test. Ducks were deprived of food one hour before each test, and could feed ad libitum on poultry pellets between trials. During each trial, water was available *ad libitum* at a distance of 1.80 metre from the food, which consisted of either pure wheat, or wheat mixed with an equal volume of moistened peat. For standardisation, wheat was previously oven-dried and a constant mass of 100 g of grain was presented to the ducks. Trials lasted approximately 10 minutes (from presentation of the food to the moment when all birds turned to non-feeding activities) and not all birds engaged in feeding behaviour during a trial. In no case the whole food was consumed at the end of a trial. Sieved peat was moistened and added to the wheat to make a sticky mixture that prevented the ducks from sorting the grains. Peat was chosen because its texture mimicked that of the natural substrate when moisten.

In a second experiment, we measured the effect of water deprivation on the daily food intake of mallards. We individually isolated 9 ducks in 3m^2 individual enclosures for 24 hours. In each trial we gave either 100g dry mass of pure wheat or 100g dry mass of wheat mixed with an equal volume of moistened peat to each individual, with water in a bowl 1.80 metre apart from the food or without water. The following day, we collected the food that had not been eaten, weighed it after drying to constant mass at 80°C, and calculated the amount of wheat that had been consumed. We repeated the procedure twice for each individual and each experiment. The amount of peat ingested could not be measured since we had to wash it out with water to isolate the wheat that had not been eaten.

Field observations

We collected data during daylight hours on two sites in western France (45°60' N., 01°00'W.) with contrasting characteristics: the sewage works of Rochefort and the Nature Reserve of Moëze. The study pond at the sewage works consisted of a 6.5 ha freshwater pool bordered by a reedbed (inaccessible to ducks for foraging purposes), with flat islets covered by herbaceous vegetation. Water depth was approximately 15 cm except in a bordering ditch. The site was visited by 13 Mallard on average (±1 SE, *n* = 114 counts), 30 % of foraging individuals (± 0.1 SE, *n* = 92) were feeding on dry land.

The study site in the Reserve of Moëze was a 32 ha partly flooded polder bounded by a sea-wall, which had been used for the production of salt until the very early 20th century. Water depth exceeded 25 cm in most of the site. Vegetation on dry land was accessible to ducks on the sides and the top of the banks between the salines, from one to two metres high. The site was used by 308 Mallards on average (±23 SE, *n*=143 counts), 51% of foraging individuals (±0.1 SE, *n*=97) were feeding on dry land.

Behavioural observations combined focal individual and scan samplings (Altman 1974). From October 1995 to February 1996 and from October to December 1996, foraging Mallards, chosen at chance, were observed individually for 10 minutes with a x20 telescope between 0800 and 1800 hours. The behavioural sequence of the duck was recorded continuously. Within each sequence each behaviour was given to the nearest 0.5 second. We distinguished between vigilance (*ie* alertness), aggression, feeding and walking, as well as time spent in the water.

Feeding sessions refer to the time spent actively feeding between two visits to the water. This does not include the duration of vigilance and agonistic behaviour. Interruptions refer to the time spent walking to the water, the time spent on the edge with the bill in the water, and the time walking back to the feeding ground. The time spent on the shore included only times when the duck had its bill in the water, not vigilance or agonistic activities. We recorded separately the time taken to walk to and from the water (hereafter walking trips). The duration of walking trips towards the water was used as a measure of the distance from the water at which a duck was feeding because ducks walked straightforward to the shore after each feeding session. Focal individual samplings were performed on 18 Mallard at Rochefort and 13 at Moëze. All ducks regularly alternated feeding with walking trips to the water. In order to avoid individual pseudoreplication, only the mean data of each focal individual was used in the analyses.

Scan samplings were performed regularly throughout daylight hours at both sites from September to December 1996. We distinguished Mallards which were feeding and, among them, the number of individuals foraging on dry land to measure the use of terrestrial feeding methods among foraging birds. Each site was visited one day per week. Data from each study day were averaged to obtain a weekly value. The number of weekly data is 14 at Rochefort, but 11 at Moëze where the study site was only partly flooded in the first three weeks and not used by Mallards for foraging. Values are given as means ± SE throughout the paper.

Results

Food consumption in captivity

Captive Mallards given pure wheat consumed one large meal before going to the water. Each feeding session lasted 25.8s ± 3.03 (n=20). They never returned to eat a second time.

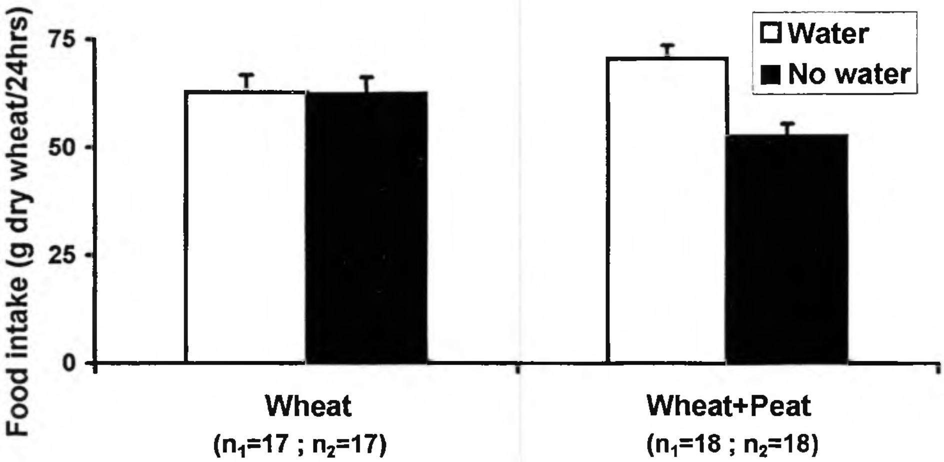

Figure 1. Daily food consumption of Mallard feeding on the two types of experimental foods, with and without water. Vertical bars show standard errors. Numbers in brackets are sample sizes. The food intake on wheat plus moistened peat without water differed significantly from other food intakes (see text for statistics).

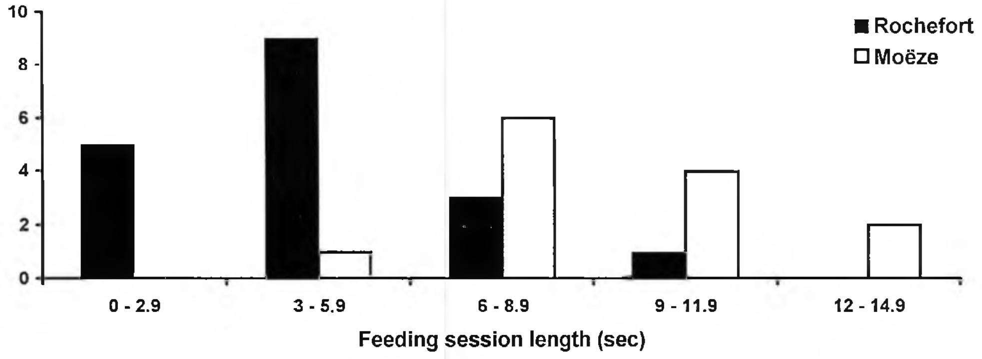

Figure 2. Distribution of feeding session length of terrestrial feeding Mallard at Rocheford (n=18) and Moëze (n=13)

By contrast, ducks feeding on wheat plus moistened peat regularly interrupted feeding, and filtered food from peat in the water. Feeding sessions were shorter in this experiment than when ducks were feeding on pure wheat (9.3s±0.98, n=20, t-test: t=5.08, P<0.0001). Birds returned to the food source 3-15 times.

Results of a 2-way ANOVA with type of food (*ie* wheat or wheat plus peat), treatment (*ie* water available or no water) and the interaction Food x Treatment as independent variables showed that food intake did not differ between food types (F=0.11, df=1,66, P=0.74) but differed between treatments (F=7.0, df=1,66, P<0.05). The significant effect of the interaction of food and treatment (F= 6.52, df=1,66, P<0.05) showed that differences were due to a lower food intake on wheat plus peat in the absence of water than with water available (**Figure 1**), since water deprivation led to a 26% decrease of the food consumption.

Terrestrial feeding by Mallard

A large proportion of Mallards fed on land both at Rochefort (30% ± 0.04, n=92) and at Moëze (51% ± 0.04, n=97).

Ninety-four percent of the feeding sessions at Rochefort, and 61 % at Moëze, lasted less than 10 seconds (**Figure 2**). Feeding sessions lasted 4.4s ± 0.5 (n = 18) at Rochefort, and were more than twice as

Table 1. Walking trip duration (in seconds) at Rochefort and Moëze. Values are means ± SE. Numbers in brackets are sample sizes.

Site	Direction	
	to the water	to the feeding patch
Rochefort (n=18)	0.8 ± 0.2	1.6 ± 0.3
Moëze (n=13)	2.0 ± 0.3	3.3 ± 0.5

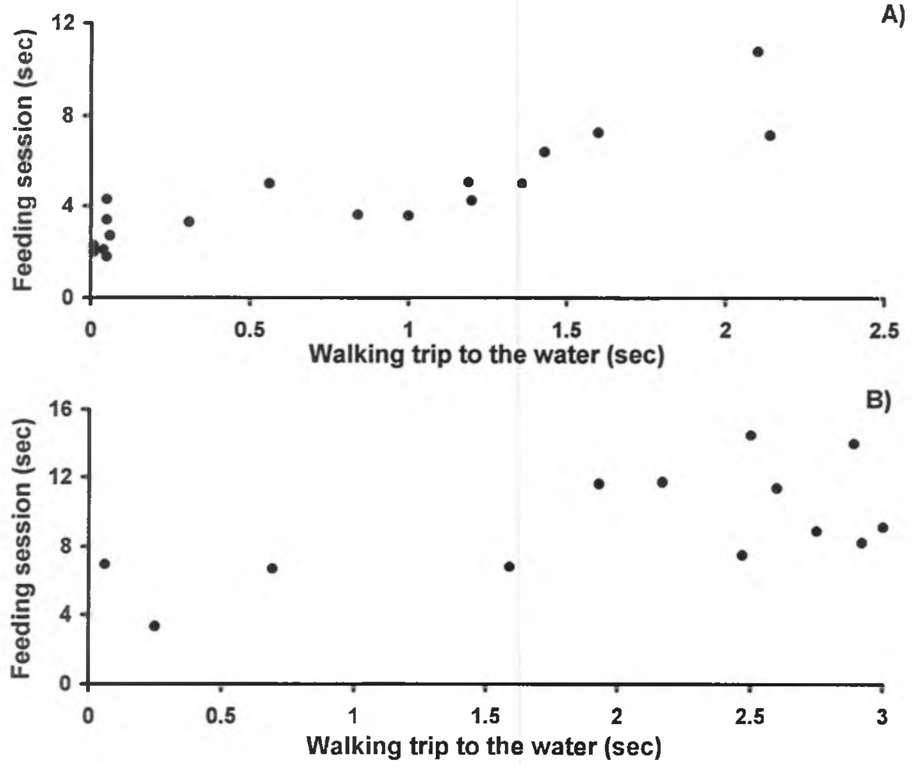

Figure 3. Relationship between the mean length of feeding sessions and the distance from water (expressed as the length of walking trips to the water) at A) Rochefort and B) Moëze (see text for statistics).

long at Moëze (ie 9.3s±0.9, *n*=13, t-test: t=20.7, *P*<0.0001). The length of feeding sessions increased with increasing duration of walking trips from the feeding grounds to the water, both at Rochefort (*Y*=2.34 + 2.69*x*, F=51.27, r^2=0.76, df=16, *P*<0.0001) and at Moëze (*Y*=5.34 + 1.99 *x*, F = 7.71, r^2 = 0.41, df=11, *P*<0.05; **Figure 3**). An ANCOVA with 'Site' as a factor and 'Walking duration' as a covariate showed that, although feeding sessions were significantly longer at Moëze (Site: F = 51.14, df = 1,27, *P*<0.0001), slopes of the regressions did not differ between sites (Site x Walking duration: F = 0.77, df = 1,27, *P*=0.39). No focal individual had feeding sessions longer than 15 seconds on average.

No focal individual had walking trips to the water longer than 3 seconds on average (**Figure 4**). Walking trip duration to the water and to the feeding grounds at both sites are presented in **Table 1**. A 2-way ANOVA showed that walking trip duration differed between sites (F=19.68, df=1,58, *P*<0.0001), between directions (ie to the water or to the feeding grounds: F=10.31, df=1,58, *P*<0.01), but that the pattern of longer walking trips to the feeding grounds than to the water did not change between sites (Site x Direction: F=0.65, df=1,58, *P*=0.42). The time spent at the shore increased with increasing length of the previous feeding session at Rochefort (*Y*= 0.74 + 1.57 x, F=19.63, r^2=0.55, df=16, *P*<0.001) while the

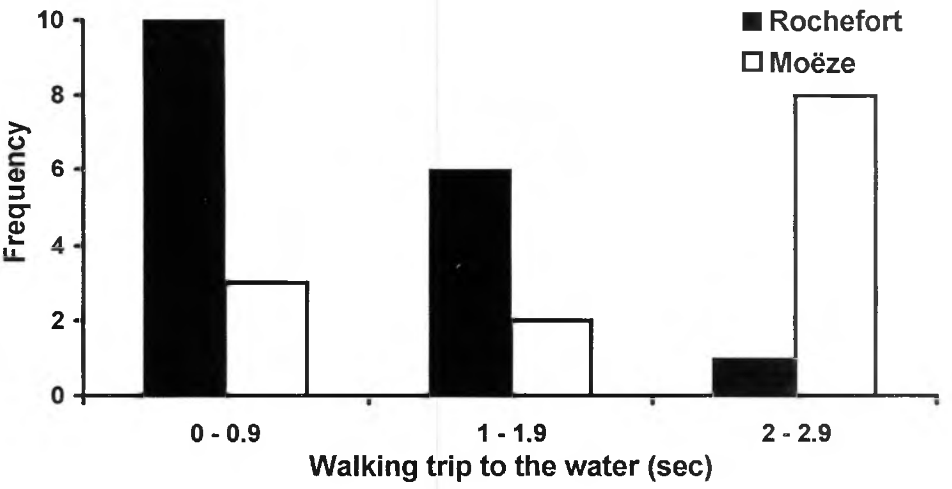

Figure 4. Distribution of walking trip length to the water by Mallard at Rochefort (n=18) and Moëze (n=13).

relationship was not significant at Moëze ($F<0.01$, df=11, $P=0.99$).

Discussion

Why Mallards interrupt feeding sessions

Mallards in the field regularly interrupted feeding to go to the water. This is unlikely to be an anti-predator strategy, since ducks interrupted their feeding both when foraging close and far from the water, thus at varying levels of predation risk (see Mayhew & Houston, 1989, concerning Wigeon). This behaviour was observed both in a brackish and a freshwater area, suggesting that ducks did not use water because of salt in their diet.

The fact that Mallards regularly interrupted their feeding suggests that the taking of water is a part of their feeding process. It is known that water is needed for digestion in birds (Duke 1986b). However, if water was needed for the digestion *sensu stricto* only, ducks should not need to interrupt their feeding as frequently as observed here. They seemed to have an immediate need for water after the prehension of the food, thus in the ingestion phases of the feeding process.

Ducks feeding on pure wheat consumed a large quantity of grain in one feeding session. This proves that Mallards are able to ingest wheat, and presumably other seeds, without water. Consequently, we conclude that interruptions observed in the field are not performed in order to take water to swallow the food.

A 24 hours water deprivation did not affect daily food intake of birds given pure wheat, suggesting that ducks could both ingest and digest their food without a frequent water intake. Ducks probably relied on internal water, according with previous studies showing that ducks could easily tolerate 36 hours without drinking (Harvey *et al.* 1981). The fact that ducks interrupt their foraging so frequently in the field is not caused by a constraint during the manipulation of food in the bill, during the ingestion phase, or a physiological need during digestion.

When fed with wheat plus moistened peat, Mallards interrupted feeding regularly and were observed to use water to filter the grain from non-digestible material, which were sieved through the bill lamellae. Ducks had a 26% lower daily food intake in the absence of free water. We conclude from this that the absence of water affects food intake because it prevents the ducks from washing off the indigestible particles, and that the behaviour observed in the field is a tactic developed in order to avoid the ingestion of such particles. Several hypotheses can be invoked to explain the reduction of food intake, such as a digestive bottleneck (Kenward & Sibly 1977) through space occupation in the digestive tract, or the digestion being hampered by the ingestion of reduced matter when drinking is not possible. The question of how non-digestible material affects food intake will need further experimental work.

Terrestrial feeding in nature

Terrestrial feeding is a common behaviour of granivorous ducks in agricultural environments (*eg* Krapu 1974; Thomas 1981; Jorde *et al.* 1983; Baldassarre & Bolen 1984). Our results show that Mallards also use this foraging tactic in natural conditions, and can feed on dry land for more than half of their foraging time. Interruptions accounted for a large part of the total feeding time when Mallards fed on dry land. Ducks feeding underwater also filter their food (Tamisier 1972; Thomas 1982). These birds thus also suffer a reduction of foraging time, but the cost is lower due to the absence of time and energy losses of walking between the feeding patches and the water.

Mallards feeding on dry land lengthen their foraging sessions when feeding farther from the shore, at both sites. It is likely that this is to collect a larger amount of food per session as the cost of interruptions increases. Ducks spend more time filtering their food at the shore at Rochefort when the previous feeding session is longer, which suggests that more material had been collected and supports this hypothesis. However, the relationship was not significant at Moëze. This does not imply that the above hypothesis does not apply: if the amount of available food is lower at this site, Mallards could still increase the length of feeding sessions when foraging farther from water but this would simply not always be successful, and filtering time will not increase systematically as feeding time increases. Several observations give weight to this: the fact that feeding sessions were longer at this site could be related to a longer searching time in poorer conditions, and the presence of much more individuals at Moëze is likely to increase the rate at which the food is depleted.

The behaviour of ducks could differ farther from water because of higher food depletion close to the shore. However, if more food was available, ducks would be able to collect more in each feeding bout, would not increase the length of their feeding sessions and would filter for longer times with increasing distance from water. Because feeding sessions are longer when feeding farther from the shore, our results weekly support this alternative hypothesis.

Our experiments show that, when water is available, Mallards do not ingest their bolus before filtering it when food is mixed with non-digestible material. The length of foraging sessions in the field is thus limited by the volume of the bill, and can thus not increase indefinitely with increasing distance from water. As a consequence, ducks should select feeding patches closer to the shore. Indeed all the feeding birds were observed to forage in patches less than three seconds walking from the water on average, roughly five metres from the shore.

The reason why walking trips to the feeding grounds took a longer time than walking trips to water is unclear: grassland areas are generally more elevated than the surface of the ponds, and it may be more difficult for ducks to "climb" to the feeding grounds than to go down to the water. Visual detection of food could also occur, and ducks may search for food during walking trips to the feeding grounds. On the other hand, the reason why walking to the water took shorter time than walking to the feeding grounds may be related to the fact that water is the only thing mattering for ingestion when the food is acquired. Further, the shortening of walking trips to the water decreases the cost of interruptions without altering foraging efficiency.

These results could have implications for nature reserve management: granivorous dabbling ducks do not only feed in the bottom of water-bodies, but also use the banks and grasslands around them. This is the case for Mallard, and the same pattern is also observed in Pintail and Teal on some occasions. In this situation water is frequently needed, and should be present close to the feeding patches if they are to be used efficiently. Only a narrow strip of vegetation around the water-bodies can thus be exploited (approximately five metres in our study). In order to increase the area which can be used efficiently, water-bodies should have indented instead of regular shapes, so that the feeding grounds around them are closer to the water.

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