

Shape and sources of variations of the functional response of wildfowl: an experiment with mallards, *Anas platyrhynchos*

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Understanding the variations of the functional response of an organism, i.e. the predation rate in relation to prey density, is necessary to understand the interactions between the animal and its food supply. This has received little attention in dabbling ducks so we investigated experimentally the shape of the functional response of mallard feeding on poultry pellets, and assessed the influence of several factors such as the size of food items, sex or individual performance on this functional response. Individual differences in intake rate are of crucial importance in group or gregarious foraging species.

We used two approaches of the functional response: 1) the relation between feeding rate (pellets/s) and pellet densities (pellets/m²), and 2) the relationship between instantaneous intake rate (g/s) and biomass density (g/m²). For both approaches, we found that the Type II functional response gave better estimates than a Type I linear functional response but explained only a third of the variance. Our results show that pellet size has a large effect on instantaneous intake rate. The comparison of the functional response parameters suggest that handling time per prey may not reflect the real constraints on intake rate, but that handling time per gram ingested may be more appropriate to integrate the effect of item size in the functional response. We then discuss the possible mechanisms involved. We also found individual variations in the functional response for each of the experiments, with some consistency in the hierarchy regarding feeding efficiency. We did not find any differences between males and females.

Our results provide an evaluation of individual variations in intake rate in interference-free conditions, which has rarely been done, and call for more controlled experiments to allow a finer understanding of the mechanisms of food acquisition in dabbling ducks.

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Measuring and understanding the causes of variations of the functional response of an organism, i.e. instantaneous predation rate in relation to prey density (Holling 1959), have direct consequences for the understanding of ecological processes at the individual level, such as the role of dominance and interference on foraging efficiency (Goss-Custard et al. 1984, Stillman et al. 1996, Norris and Johnstone 1998), and to evaluate the role of these individual differences at the population level (Rubenstein 1981, Goss-Custard et al. 1995, Piersma et al. 1995). There are several

mechanisms that can generate the various functional responses, particularly the asymptotic part: the competition between handling and searching for a prey, but also the interference between harvesting food and the velocity of the animal, or the competition between cropping and processing food (see Spalinger and Hobbs 1992 for the theoretical approach on herbivores). The understanding of the shape and parameters of the functional response can thus allow for the testing of hypotheses related to processes limiting intake rate (Gross et al. 1993).

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Analyses of functional response have been applied to various exploitative systems such as host-parasitoid, plant-herbivore systems and waders (e.g. Hassell 1978, Crawley 1983, Wanink and Zwarts 1985, Spalinger et al. 1988, Piersma et al. 1995). This aspect of feeding ecology has received little attention in dabbling ducks. One of the possible explanations for this lack of studies is the wide variety of feeding techniques that dabbling ducks may use, including filter-feeding and pecking, or even scooping for food in various positions at various depths (Thomas 1982). Although most dabbling duck species are not really adapted to pecking due to the modification of their bill anatomy to allow filtering (Kooloos and Zweers 1991), this behaviour is frequently recorded, particularly when ducks are feeding in crop fields (Gillespie 1985, Baldassare and Bolen 1995). We developed a set of experiments to investigate the shape of the functional response of mallard feeding in dry patches, i.e. ducks would have to peck or scoop for their food, and identify some sources of variations of the response such as food item size, sex or individual performance. This experimental approach allowed for the measurement of individual variations in intake rate, which is central in group or gregarious foraging species and has implication for their population dynamics (e.g. Bjørnstad and Hansen 1994, Goss-Custard et al. 1995, Sutherland 1996).

The most common functional response in simple predator-prey systems is the Type II of Holling's original classification (Holling 1959, 1965). The model most frequently used for this monotonically decelerating functional response is the 'disc' equation:

$$FR = AN / (1 + ANTh) \quad (1)$$

where FR is the intake rate (number of preys/unit of time), A is the searching efficiency of the predator (m^2 /unit of time), N is the density of food (preys/ m^2) and Th is the time to handle the prey once it has been captured. This equation has also been adapted to incorporate the weight of the prey captured and express the relationship between intake rate (IR, g/unit of time) and food biomass density (g/m^2), and this has been proved very appropriate for animals taking several prey per mouthful, e.g. herbivores (Spalinger et al. 1988). Dabbling ducks may take several items per mouthful, probably in relation to item size, so we used the two approaches of the functional response for mallard: 1) the relationship between feeding rate and food item density, and 2) the relationship between instantaneous intake rate and the biomass density of food.

Because the shape of the functional response has been found to be linear, i.e. Type I ($IR = AX + B$), in few empirical studies on small vertebrates (e.g. Batzli et al. 1981) and appeared close to linear for filter-feeding teal (van Eerden and Munsterman 1997) we also tested for the existence of a Type I response in mallard.

Methods

Experiments

All experiments were carried out in February and March 1997 at the Centre d'Etudes Biologiques de Chizé, 60 km east of La Rochelle on the French Atlantic coast. We used 14 ducks (7 females and 7 males). Every individual belongs to a third generation of ducks caught in the wild and had been at the laboratory for at least 6 months before the start of the experiments. The enclosure in which ducks were kept comprised 100 m^2 of grass, a 25- m^2 pond and 100 m^2 of concrete floor with a 25- m^2 enclosure where the trials were carried out.

We made three sets of trials with poultry pellets as food. We used three different pellet sizes to test for an influence of item size on the shape of the functional response: small (1×2 mm, 0.0079 g), medium (3×4 mm, 0.044 g) and large (4×7 mm, 0.134 g). To be able to compare the functional response between these different pellet sizes, we varied food availability: we presented 0.5- m^2 patches with ten different food masses: 10, 20, 30, 40, 50, 75, 100, 150, 200 and 300 g. One patch at a time was presented to one individual duck. We weighed the food remaining in the patch after each trial to measure the amount of grain eaten and calculated instantaneous intake rate (in g per seconds spent feeding, *sensu* Lendrem 1984). We recorded the time spent feeding in the patch and we stopped the trial at 60 s. Some individuals stopped feeding earlier, though food was still available. This was often linked to a disturbance caused by human activities in the vicinity of our experimental grounds. The minimum time feeding considered to calculate intake rate was 40 s; only 15% of our values were between 40 and 60 s. We also had individuals that did not stop immediately when we moved towards them at the end of the session, leading the feeding time to actually exceeding 60 s: 20 of our values were between 60 and 70 s. The delay in starting to search for food in the patch varied from 5 s to 2 min according to individuals and days, and we considered that after 3 min without paying any attention to the patch the trial was aborted. Some delays were due to outside disturbances, but it is also possible that these delays reflected differences in hunger between the individuals, which would have affected our measures of intake rate. However, because we randomised the order in which ducks and densities were tested, it is unlikely that there was a systematic individual bias in hunger that would be the only cause for individual differences in intake rate.

Royama (1971) showed that the disc equation cannot properly model the functional response of the predator unless the prey density is unchanged during the time frame during which the animal feeds. However, changes in both feeding rate and instantaneous intake rate (g/s

feeding) can still be described with this equation providing that the experiments do not last too long in order to avoid the depletion process. Accordingly, as we stopped the experiment when feeding time reached 60 s, we prevented patch depletion to occur at low densities. At the lowest density, 10 g, we checked if intake rate changed with time feeding in the patch to control for the potential effect of food depletion: no trend was found in any of the trials (linear regression, all $P > 0.28$).

We performed the trials with the individual isolated from the group to minimise social interference, but visual contact with the other birds was still possible. Some individuals did not feed at all pellet densities. Those individuals that did not feed for at least six pellet densities for a given experiment were not included in the analysis for that experiment.

Statistical analyses

For each pellet size, the biomass offered corresponded to a known pellet density, so we investigated the shape of the functional response both for pellet biomass and pellet density. We tried first to fit a Type II functional response for each of the four experiments using a SAS NONLIN Procedure (SAS Institute 1990), and compared the fit with a linear regression by comparing the coefficient of determination, R^2 , coefficient of variation, CV, the biological relevance of parameter values and their standard errors if necessary (Juliano and Williams 1987, Lundberg 1988). The R^2 were calculated with the corrected sum-of-square (Motulsky and Ransnas 1987) and we used all individual points to allow a better estimate of the parameter values (Juliano and Williams 1987). The use of the biological criteria is crucial to determine between models that generate similar R^2 and CV (Lundberg 1988). We used the classical Type II equation derived from Holling's disc equation (1) for feeding rate and instantaneous intake rate. Still following Lundberg's comparative approach of different functional response types, we verified that depletion was not affecting our measures by comparing the fit and the parameter estimates of the 'classic' Type II with the 'random predator' equation (Royama 1971, Rogers 1972) that models appropriately a system where the initial prey density actually decreases during the course of exploitation by the predator:

$$FR = (N/T)\{1 - \exp[-A](T - NaTh)\} \quad (2)$$

where T is the time spent foraging in seconds and Na is the number of preys harvested during T . This equation has its equivalent for intake rate with Na being the number of grams harvested per seconds.

Once we made the comparison between the various functional responses, we selected the best, which was

the 'classic' Type II, and compared the functional response between experiments in order to evaluate the influence of pellet size on intake rate and feeding rate. We then compared the residual values of each individual to assess if there were differences between individuals in their response to changes in food availability. To assess whether it was always the same individual that was performing better, we ranked animals following the values of the mean of residuals: the highest mean value would be ranked 14, and we calculated Kendall coefficient of concordance in ranks, W (Sokal and Rohlf 1995). We compared means and variances using the SAS GLM Procedure (SAS Institute 1990) when the sample size and the homogeneity of variance allowed it, if not we used non-parametric Kruskal-Wallis test (SAS NPAR1WAY Procedure, SAS Institute 1990). We then fitted the Type II functional response to each individual and obtained individual values of A and Th . We compared the means of A and Th for the various sets of experiments using non-parametric Kruskal-Wallis tests to evaluate which parameters influenced the most changes in the functional response. In order to test for a possible effect of sex on the functional response, we performed an ANOVA on the residuals with sex as a factor and individuals nested within sex as the error term following the repeated measurement option of the SAS GLM Procedure (SAS Institute 1990: 952).

Results

Shape of the functional response

The Type II functional response fitted our data well for each set of experiments, both for pellet biomass and pellet density, but only explained between 30 and 47% of the variance (Figs 1, 2, Tables 1, 2). The 'classic' type II modelled by Holling's disc equation was only slightly better than the linear regression in fitting our data, with R^2 higher for the Type II equation than for the Type I. However, the linear regression generated equations with positive y -intercepts that differed significantly from zero (all $P < 0.05$) which is not consistent with biological reality. Our results thus suggest that the functional response of mallards is a Type II shape rather than a Type I. The 'random predator' equation failed to describe our data for feeding rate but showed an adequate fit for intake rate in two sets of experiments. However, it could not produce realistic estimates for handling time Th (i.e. Th always negative and/or greater than total time irrespective of iteration methods used). This does not imply that the 'Random predator' approach does not apply to dabbling ducks but rather that our experiments adequately reflected values of instantaneous intake rate, i.e. with a minimised influence of depletion on instantaneous intake rate during our trials.

Effect of pellet size on the functional responses

Feeding rates were 10 times higher for small than for large pellets (Fig. 1); however the values of intake rate for large pellets were systematically above the two others for all food biomass densities (Fig. 2), the differ-

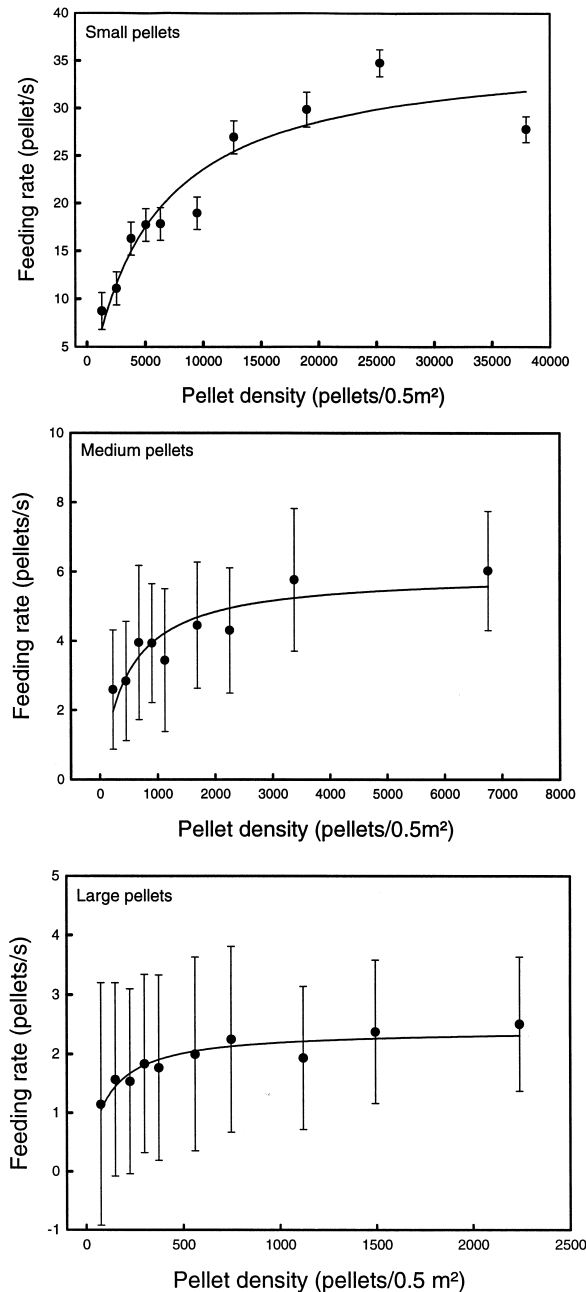


Fig. 1. Relationship between the feeding rate (pellets/s) and pellet density (pellets/0.5 m²) for mallard feeding on three different pellet sizes. This represents a Type II functional response, dots are means \pm SE, the line is the results of the fit of Holling's disc equation (parameters in Table 1).

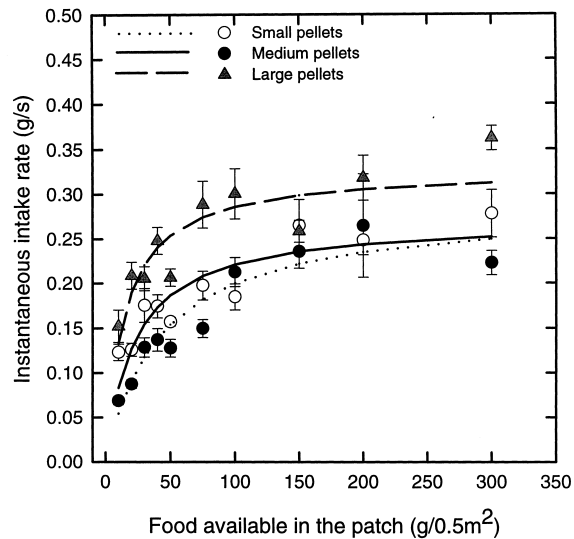


Fig. 2. Relationship between instantaneous intake rate (g/s) and biomass density (g/0.5 m²) for mallard feeding on three different pellet sizes. This represents a Type II functional response, dots are means \pm SE, the line is the results of the fit of Holling's disc equation (parameters in Table 2).

ence being significant for eight densities (all ANOVA $P < 0.01$ except for 150 g and 200 g where $P > 0.05$). The medium size pellets seem to induce a higher intake rate than the small ones at low densities (all $P < 0.05$ from 10 g to 75 g), but the patterns were unclear for high densities ($P > 0.05$ except for 300 g where $P < 0.05$). The fact that the hierarchy of feeding rate and intake rate curves were inverted between pellet sizes (Figs 1, 2) strongly suggest that food item size played a crucial role in determining intake rate.

From these differences between feeding rate and intake rate we could expect differences in the values of the parameters of the functional responses. For feeding rates, the estimated handling time, Th , varied between pellet sizes (Kruskal-Wallis $\chi^2_{\text{approx}} = 29.2$, $df = 2$, $P = 0.0001$, Table 3) and search rate also was significantly different between pellet sizes (Kruskal-Wallis $\chi^2_{\text{approx}} = 14.9$, $df = 2$, $P = 0.0006$, Table 3). For intake rates, handling time did not vary between the different pellet size (Kruskal-Wallis $\chi^2_{\text{approx}} = 4.26$, $df = 2$, $P = 0.119$, Table 4). Conversely, search rate remained significantly different between pellet size (Kruskal-Wallis $\chi^2_{\text{approx}} = 14.9$, $df = 2$, $P = 0.0006$, Table 4).

Individual variations in the functional response

Individuals showed different responses to variation in food availability for all pellet sizes, but the overall shape remained that of a Type II (all corrected $R^2 > 0.80$, Fig. 3). The comparison of the residuals of each

individual to the general functional response showed that inter-individual differences existed for each of the experiments ($F_{9,98} = 2.06$, $P = 0.040$; $F_{10,77} = 2.02$, $P = 0.043$; $F_{12,128} = 4.11$, $P = 0.0001$; for small, medium and large pellets, respectively). These differences explained ca 20% of the variance around the functional response of our group of captive mallards for each set of experiments. To investigate which individuals were having different values of residuals for each trial we used the Tukey test for multiple comparison and found that few of the individuals differ significantly (Table 5). Further, we then tested for correlation between the ranks of the nine individuals that participated to all trials to assess whether there was a pattern and that some of them tended to be consistently better than others. We found a concordance between the rankings of individuals in the three sets of trials (Kendall $W = 0.707$, $\chi^2 = 16.97$, $df = 8$, $P < 0.05$). When we tested for the effect of sex in addition to that of individuals, we found no significant difference in any of the experiments (Repeated ANOVA, all $P > 0.12$).

Discussion

The functional response and pellet size

In this study we have extended the analysis of the functional responses to include a dabbling duck, the mallard feeding on poultry pellets of different sizes. A type II functional response seems adequate to describe the relationship between feeding rate or instantaneous intake rate and changes in food availability (density or biomass). The non-linear shape of the functional response reflected the fact that food intake rate was ultimately limited at high densities (see below for further discussion on limiting factors). The few cases with

vertebrates showing linear functional responses were recorded in resource-poor ecosystems, e.g. reindeer (*Rangifer tarandus* (L.); White et al. 1981) or brown lemming (*Lemmus sibiricus* (Kerr); Batzli et al. 1981), and there are reasons to believe that most vertebrates in these systems are limited by resource abundance well before they can experience a limitation by food processing. The fact that van Eerden and Munsterman (1997) found a linear relationship for filter-feeding teal may be explained by the pumping ability of dabbling ducks which allow them to maintain a high seed intake rate; Kooloos and Zweers (1991) had difficulties in finding limits in food processing for filter-feeding mallards in their experiments.

The feeding conditions used in our experiments are those encountered by wild dabbling ducks when feeding on crop residues in cultivated fields, a common food source in their winter quarters (e.g. Bossenmaier and Marshall 1958, Baldassare and Bolen 1984). The values of instantaneous intake rate we measured compare well with the average intake rate recorded for mallard in feeding experiments on threshed cereal heads: 0.07 g/s for a density of 15 g/0.5 m² (Clark et al. 1986a), while our values of instantaneous intake rate at low biomass densities for small pellets (10 and 20 g/0.5 m²) lie between 0.06 and 0.09 g/s. The biomass densities used in our experiments are slightly high compared to actual figures, which rarely exceeds 70 g/m² on average (Baldassare and Bolen 1984), but may reach values between 140 and 330 g/m² (Clark et al. 1986b). Similar food biomass were reported in maize fields close to our study sites (up to 69 g/m²) but with biomass densities locally reaching 176 g/m² (Poisbleau unpubl.). Since the asymptotic values of intake rate are reached after 100 g/m², our results suggest that field feeding mallards rarely experience situations where they reach the asymptotic value of intake rate.

Table 1. Results from the fit of different models of functional response between feeding rate (pellets/s) and pellet densities (pellets/0.5 m²) for the four set of experiments.

Model	Food source	R ²	Parameter values	Asymptotic SE
Linear Type I	Small	0.237	A 0.0005 B 14.533	0.00009 1.738
	Medium	0.449	A 0.0005 B 0.3127	0.00006 0.008
	Large	0.283	A 0.00041 B 3.052	0.00006 0.175
Type II classic	Small	0.326	A 0.0067 Th 0.0277	0.0015 0.0024
	Medium	0.467	A 0.0124 Th 0.1638	0.0019 0.0082
	Large	0.302	A 0.0225 Th 0.4088	0.0038 0.0144
Type II random predator	Small	Failed		
	Medium	Failed		
	Large	Failed		

Table 2. Results from the fit of different models of functional response between instantaneous intake rate (g/s) and biomass density (g/0.5 m²) for the four set of experiments.

Model	Food source	R ²	Parameter values	Asymptotic SE
Linear Type I	Small	0.237	A 0.0005 B 0.115	0.00009 0.0137
	Medium	0.449	A 0.0005 B 0.138	0.00006 0.008
	Large	0.283	A 0.00045 B 0.209	0.00006 0.0098
Type II classic	Small	0.326	A 0.0067 Th 3.512	0.0015 0.315
	Medium	0.467	A 0.012 Th 3.689	0.002 0.184
	Large	0.302	A 0.0225 Th 3.0531	0.0038 0.1080
Type II random predator	Small	Failed		
	Medium	0.338	A 0.001 Th -1.237	0.0003 1.526
	Large	0.370	A 0.0014 Th -0.4052	0.0004 1.0117

In our experiments, pellet size had a strong influence on intake rate. This had already been shown experimentally for Japanese quail (*Coturnix coturnix japonica*) for which meal frequency, meal size and therefore intake rate were affected by changes in pellet size (Savory 1980). Large seeds also seemed to allow high instantaneous intake rate in filter-feeding teal, leading the ducks to actively select for these large items (van Eerden and Munsterman 1997). When feeding on dry food, mallard are expected to be more efficient, i.e. have a higher intake rate, on large (6–8 mm) than on small seeds (1–3 mm) because transport of food items in the bill is more effective (Kooloos and Zweers 1991). This may explain why large pellets allow higher intake rate, at least in comparison to small pellets.

Another limiting factor in food harvesting by dabbling ducks is the amount of food items that can be grasped in one time to fill the rostral cavity of the bill (Kooloos and Zweers 1991). This is constrained by the volume of the cavity and the size of the items. Since we are interested in intake rate (g/s), the weight of the mouthful is also likely to play a role, independently of the number of items contained in the mouthful. Unfortunately, we did not manage to measure peck size since the ducks often varied from pecking, scooping or even skimming the pellets during a trial. However, the contrasted results between feeding rate and intake rate support the idea that item size could have a major influence on intake rate through the size or the weight of the mouthful. Despite the great difference in the calculated handling time per item (Table 3), the handling time per gram did not differ (Table 4), i.e. one mouthful of small pellets and one mouthful of large pellets with similar mass have the same handling time. Handling time per gram ingested thus appears a better assessment of the costs associated to the choice of various prey types, a conclusion also reached for oys-

tercatchers, *Haematopus ostralegus*, feeding on a wide range of prey types (Zwarts et al. 1996).

Our results thus suggest that it was not really handling the food in the bill that constrained intake rate but rather the amount of food collected in one mouthful (i.e. peck size). This would imply that it is easier to take big mouthfuls on large food items than on small ones for a given biomass available (i.e. when small item density is much higher than large items). This is consistent with the fact that in our experiments, the difference in intake rates between pellet sizes was mainly influenced by *A*. In our experiments the food was visible, hence it was cropping the food that mattered rather than searching it. The differences in the parameter *A* reflected differences in the speed at which the asymptotic value of intake rate is reached, i.e. difference in maximum cropping rate (g/s, *AN*), for a given biomass. These differences in values of parameter *A* should have an impact on the rate at which food supplies are depleted. Simulations carried out for oystercatchers feeding on mussels, *Mytilus edulis*, showed that the rate at which maximum intake rate was reached conditioned the percentage of the population starving, hence the proportion surviving through the winter (Goss-Custard and West in press).

Table 3. Average values of calculated search rate *A* and handling time *Th* from the functional response between feeding rate (pellet/s) and pellet density. The figures are the means of individual parameters values estimated from the type II functional response for the four different experiments (parameter values with the same letter do not differ significantly, Kruskal-Wallis test, *P* > 0.05).

Experiment	Search rate (SE)	Handling time (SE)
Small pellets	0.0080 (0.0040) ^a	0.032 (0.027) ^a
Medium pellets	0.0166 (0.0039) ^{ab}	0.163 (0.026) ^b
Large pellets	0.0219 (0.0037) ^b	0.411 (0.025) ^c

Table 4. Average values of calculated search rate A and handling time Th from the functional response between instantaneous intake rate (g/s) and biomass density (g/0.5 m²). The figures are the means of individual parameters values estimated from the Type II functional response for the four different experiments (parameter values with the same letter do not differ significantly, Kruskal-Wallis test, $P > 0.05$).

Experiment	Search rate (SE)	Handling time (SE)
Small pellets	0.0077 (0.0039) ^a	3.890 (0.410) ^a
Medium pellets	0.0160 (0.0038) ^{ab}	3.716 (0.399) ^a
Large pellets	0.0227 (0.0025) ^b	3.074 (0.271) ^a

From these results, we suggest that, in the wild, dabbling ducks are unlikely to reach their maximum intake rate and that their instantaneous rates of food intake are primarily limited by food abundance, with the possible exception of particular feeding conditions where sorting food items from non-alimentary particles requires long sieving sessions in the water (Guillemain et al. 1999). However, we have to bear in mind that results of functional response tests in an oversimplified experimental situation should of course be treated with caution when applied to the real world (Abrams 1982).

Individual variations in the functional response

Our experiments showed that individuals varied in their functional responses, i.e. intake rates. In Harper's experiment (Harper 1982), the fact that individual mallard vary significantly in resource acquisition was attributed to the differences in dominance rank, which provided access to the best patches, but no information was available on the foraging efficiency of individuals. Similar results were found in oystercatchers where dominance seemed not to be related with feeding efficiency but dominant individuals were less affected by interference in their intake rates (Stillman et al. 1996). In our study, ducks were tested in isolation, which implies that the differences in intake rates were independent from social interactions. Some of the differences between individual intake rates may be due to the state of the animal at the time of the trial, but the fact that individuals differ in their intake rates across a wide variety of feeding conditions strongly support the idea of real individual differences. The fact that the hierarchy of individuals in foraging efficiency was consistent across pellet size also militates for the existence of differences in the quality of individuals. Our result present the first data on differences in feeding performance in an interference-free situation, a key issue in the debate on the role of foraging efficiency as a major determinant of competitive ability in waterbirds in addition to dominance status (Caldow et al. 1999).

Since the densities we used are only found in crop fields, and rarely to such high biomass densities, we reanalysed our data on a limited set of food biomass:

from 10 to 50 g/0.5 m², which also represented realistic figures for ponds and marshes (Tamisier and Dehorter 1999). The individual differences remained for small and medium pellets ($F_{9,98} = 3.39$, $P = 0.0021$; $F_{10,48} = 2.63$, $P = 0.012$) but not for large pellets ($F_{12,66} = 1.38$, $P = 0.1984$). The latter result may reflect the fact that the constraints on intake rate were low with large pellets, hence the difference between individuals less apparent. The ranks in foraging efficiency remained not significantly correlated between small and medium pellets (Kendall Tau: $r = 0.39$, $n = 9$, $P = 0.14$)

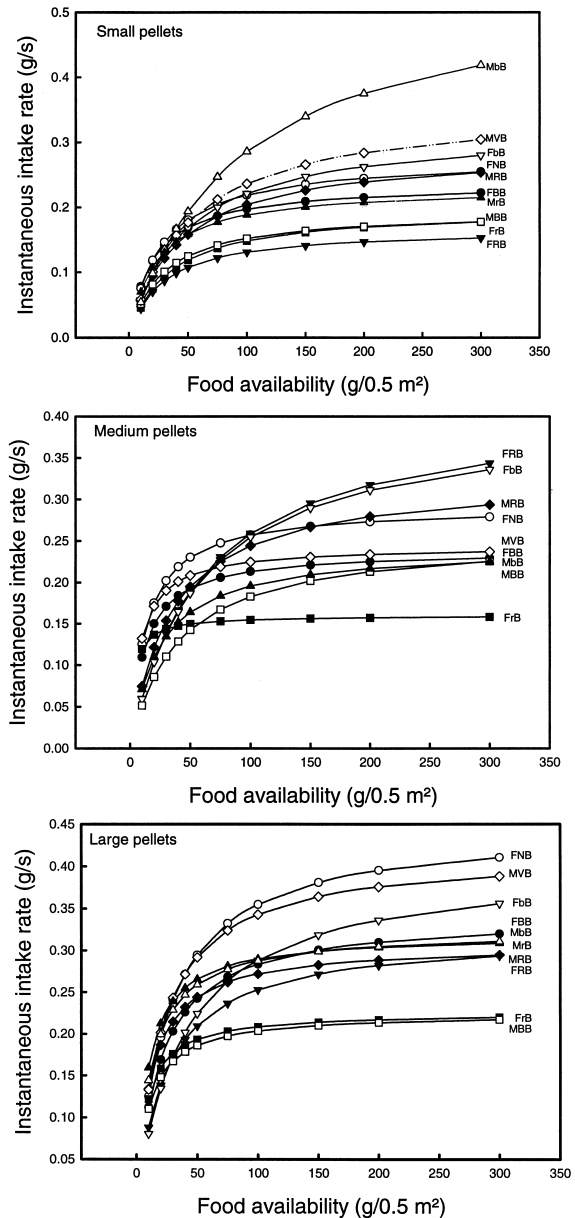


Fig. 3. Functional responses of individuals feeding on the three different pellet sizes. The relationships presented are those between intake rate and biomass density, the lines are those fitted to the individual data (all $R^2 > 0.80$).

Table 5. Average individual residual value for the three experiments (the values of average residuals with the same letter do not differ significantly, $P > 0.05$, in the Tukey multiple comparison t -test).

Individual	Average residues Small pellets	Average residues Medium pellets	Average residues Large pellets
FBB	0.0008 ^{ab}	-0.0023 ^{ab}	-0.0029 ^{abc}
FNB	0.0168 ^{ab}	0.0378 ^a	0.0468 ^a
FRB	-0.0561 ^b	0.0204 ^{ab}	-0.0320 ^{ab}
FVB	-	-	-
FbB	0.0195 ^{ab}	0.0257 ^{ab}	0.0026 ^{abc}
FrB	-0.0458 ^b	-0.0356 ^b	-0.0649 ^{bc}
F0B	-	-0.0049 ^{ab}	0.0232 ^{ab}
MBB	-0.0259 ^b	-0.0349 ^b	-0.0796 ^c
MNB	-	-	0.0340 ^a
MRB	0.0014 ^{ab}	0.0123 ^{ab}	-0.0101 ^{abc}
MVB	0.0305 ^{ab}	0.0130 ^{ab}	0.0503 ^a
MbB	0.0647 ^a	-0.0221 ^{ab}	0.0088 ^{abc}
MrB	-0.0102 ^{ab}	-	0.0021 ^{abc}
M0B	-	-0.0114 ^{ab}	0.0304 ^a

These differences in foraging efficiency may have tremendous impact on dabbling ducks in the context of their wintering quarters, particularly on the French Atlantic coast, where most of the sites used by ducks are small nature reserves that cannot support the whole population for the whole winter. The individuals performing less well may be forced to move to other feeding grounds outside the protected areas, and being more heavily exposed to predation risk or accident (Caldow et al. 1999), and in the case of dabbling ducks, to hunting pressure.

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