Foraging in a spatially patterned world
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Intake rate at differently scaled heterogeneous food distributions explained by the ability of tactile-foraging Mallard to concentrate foraging effort within profitable areas

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Jim de Fouw counting millet seeds. On the right two food distributions used in the experiment, just before the final layer of sediment was applied.
Abstract
The ability to respond to spatial heterogeneity in food abundance depends on the scale of the food distribution and the foraging scale of the forager. The aim of this study is to illustrate that a foraging scale exists, and that at larger scaled food distributions foragers benefit from the ability to subdivide a continuous (non-discrete) heterogeneous environment into profitable and non-profitable areas. We recorded search patterns of mallards *Anas platyrhynchos* foraging in shallow water on cryptic prey items (millet seeds), distributed at different scales. A small magnet attached to the lower mandible allowed us to record in great detail the position and movements of the bill tip within a feeding tray underlain by magnet sensors. Instantaneous intake rate was determined in a subsequent experiment. We successfully determined the foraging scale (about 2 x 2 cm), defined as the scale above which foragers do respond (coarse scaled distribution) and below which foragers do not respond (fine scaled distribution) to spatial heterogeneity, by concentrating foraging effort within areas of high food density. A response resulted in a significantly higher intake rate, compared to a homogeneous distribution with an equal overall density. Unlike systematic search cell revisitation was common in trials, and at coarse scaled food distributions even slightly (but significantly) more frequently observed than predicted for random search. Mallards respond to food capture by restricting displacement (area restricted search) at food distributions that are considered to be clumped for the forager (large scaled coarse distributions). We argue that partitioning the environment at the foraging scale in itself could be a mechanism to concentrate foraging efforts within profitable areas, because mallard were able to respond to heterogeneity at coarse scaled food distributions even when non-clumped (i.e. without conducting area restricted search).
Introduction
The abundance of food items is heterogeneous in space and time (Wiens 2000). The current view is that most foraging organisms benefit from this heterogeneity (Sparrow 1999). However, spatial heterogeneity can only be profitable to a forager in case it can concentrate foraging efforts within areas of high resource density (Schmidt and Brown 1996, Valone and Brown 1989) and in case benefits are not outweighed by costs to find or assess high resource density spots. Only when foragers are able to recognize spatial heterogeneity may they be able to profit from it.

Many studies show that animals indeed react to spatial heterogeneity in food abundance. Granivorous rodent species for example are able to respond to small scale heterogeneity even within discrete spatial units (patches). Fierer and Kotler (2000) and Schmidt and Brown (1996) show that animals do not need physical barriers to respond to differences in food density, but are able to place boundaries based on the food distribution itself.

Kawata and Agawa (1999) however show that foragers do not always react to existing spatial heterogeneity, depending on the spatial scale of heterogeneity and the perceptual abilities of the forager. Animals exploit the environment at a certain scale and geometry, to which we refer as the foraging scale. Animals only react to existing heterogeneity in coarse grained environments, where the scale of food distribution is larger than the foraging scale and not in a fine grained environment, where the scale of food distribution is smaller than the foraging scale. In fact, animals respond to a fine grained environment as if it is homogeneous (Kotliar and Wiens 1990).

Moreover, the foraging scale not only determines whether animals respond to existing heterogeneity, but also determines the range of food densities a forager perceives, and consequently food intake. This can be shown in a simple exercise. Imagine a one-dimensional environment consisting of a large number of small spatial units (cells). Every cell has an equal probability of containing one food item or being empty. We assume that a forager perceives food densities at the foraging scale. If we compare the perceived food densities of foragers differing in their foraging scale (number of cells sampled) there is no difference in the average food density, but the range of the detected densities differs dramatically (Fig. 1a). A forager with a small foraging scale (for example 10 cells) regularly perceives food densities larger than 0.6 items/cell whereas a forager with larger foraging scales (100 or 1000 cells) rarely perceives such densities. A forager with a small foraging scale can potentially profit from the strong heterogeneity it perceives, whereas the situation for a forager with a large foraging scale does not differ much from a homogeneous environment (Haskell et al. 2002, Ritchie 1998). If for example foragers deplete all foraging spots (with a size equal to the foraging scale) to an average of 0.5 food items/cell, the relative cumulative intake of the forager with the small foraging scale would be three times
Figure 1 A. Relative frequency distributions of food densities that foragers encounter and also perceive at different foraging scales (10 cells, 100 cells and 1000 cells) in a random environment (cells have an equal probability to contain one food item or no food item). B. Density-specific relative expected intake for foragers with a different foraging scale (10 cells, 100 cells and 1000 cells), if the food density within a foraging spot (size equal to foraging scale) is depleted to a threshold density $D_T$ of 0.5 items/cell. Relative expected intake for a certain food density $D_C$ is calculated by: $(D_C - D_T) \cdot f_{D_C}$, in which $f_{D_C}$ is the frequency in which a patch of quality $D_C$ is encountered. The surface below the curve equals the relative cumulative intake and is 0.627, 0.199 and 0.062 for foragers with a foraging scale of 10, 100 and 1000 cells respectively. If these foragers would deplete an environment consisting of 10,000 cells to an average of 0.5 prey/cells, the total number of prey they would eat are on average 627, 199 and 62 respectively.

as high as the intake of the forager with the intermediate foraging scale, and even ten times as high as the intake of the forager with the large foraging scale (Fig. 1b).

The ability to subdivide patches into smaller units is called micropatch partitioning and is limited by the foraging scale (Brown and Mitchell 1989, Fierer and Kotler 2000). Partitioning the environment at the foraging scale and subsequently depleting food density to a certain threshold level (Arditi and Dacorogna 1988, Fierer and Kotler 2000, Schmidt and Brown 1996) would result in an exploitation pattern in which foraging effort is effectively concentrated within areas of high food density. It is assumed that food density is assessed
foraging scale of tactile-foraging Mallard

at every spot during foraging, for example via instantaneous intake rate. An alternative way
to concentrate foraging effort within areas of high food density is to respond to a foraging
reward (food capture) by an area restricted search. Smith (1974) for example showed that
in an environment with a clumped prey distribution Thrushes (Turdus sp.) respond to prey
captures by displacing themselves less than was expected from the search pattern before a
prey capture. This kind of area restricted search could be a mechanism involved in
subdividing an environment into favourable and unfavourable areas, if the food distribution
is clumped (Benhamou 1992). It can even work both ways if foraging in areas of low
densities is avoided either by not changing the search path or even enlarging displacement
after a non-rewarding foraging experience (no food capture).

Many waterfowl species including mallard Anas platyrhynchos are confronted with
substantial differences in food abundance in the field and react to this (for example Nolet et
al. (2001), Van Eerden (1990)). Mallards are familiar with foraging on cryptic prey (seeds) in
a non-discrete heterogeneous environment (Cramp and Simmons 1977, Nummi 1993),
which makes them a suitable species to study the ability to concentrate foraging effort
within profitable areas.

In this study we demonstrate that mallards have a foraging scale. We explore whether
mallard concentrate their search in profitable areas when confronted with different scaled
food distributions. Our observatory technique relies on recording search paths in great detail
(tracking the bill tip at a fine scale). In a subsequent experiment we measure the
instantaneous intake rates at fine and coarse scaled food distributions to test the hypothesis
that mallards achieve a higher intake rate at scales of food distributions at which they are
able to concentrate foraging efforts within areas of high resource density.

Methods
Experiments were conducted from November 2002 to February 2003. Between trials
mallards were kept in outdoor aviaries where food (mixture of grains and pellets) was
provided after experimental trials for a period of 1-3 hours.

Study species
The six mallards (two males and four females) used in the experiments originated from a
waterfowl breeder and were 3 ½ years of age. Maximum bill length and bill width (upper
and lower mandible) of these ducks measured 51.9 (range 50.0 – 54.5), 23.5 (22.1 – 24.9)
and 15.4 mm (15.1 – 15.9) respectively. Birds weighted on average 1024 g (range 908 –
1341).

Experiment A: Foraging scale
To assess the foraging scale we determined if mallards responded to existing heterogeneity
on food distributions differing in the scale of heterogeneity (general idea similar to Kawata
and Agawa (1999)). If mallards respond to existing heterogeneity we conclude that the foraging scale is smaller than the offered scale of heterogeneity. When mallards do not respond to existing heterogeneity we conclude that the foraging scale is larger than the offered scale of heterogeneity (Kotliar and Wiens 1990). A crucial assumption to this method is that it is possible to record a potential response to heterogeneity at fine scaled food distributions. Otherwise we are unsure whether the forager does not respond to heterogeneity or that we are unable to record a response. In this experiment we are able to measure a response to small scale heterogeneity, down to the size of a food item.

**Figure 2** A. Upper view of the feeding tray. The position of the magnetic sensors is indicated by small circles. Distance between two sensors measures 1.0 cm. One example of a heterogeneous food distribution is presented (cell-width 3.0 cm). Food was only distributed in the grey shaded cells. For the analysis the sensors at the borders of these cells (grey) were excluded from the analysis for this specific food distribution. B. Head of a mallard with a small magnet mounted to the lower mandible of the bill (left) and view from below of mandible with mounted magnet to indicate position of the magnet. C. Side view of the feeding tray. Indicated are the magnetic sensors mounted in the bottom (grey shaded sensors were excluded from the analyses for this specific food distribution), two layers of sediment with a layer of food items in between (small circles) and a layer of water.
A heterogeneous food distribution was created by distributing commercial husked millet seeds on a 1 cm thick layer of sediment (mixture of aquarium sand, commercial potting clay and water; weight-ratio 4:2:1) in a Perspex feeding tray (13 x 13 x 4 cm). Mallards are able to forage extremely efficiently on millet seeds (94-98% of food is retained during filtering) and high intake rates can be achieved (average 55 seeds/s, SD 14.2) (Kooloos et al. 1989), which makes it a favoured prey type. The functional response of Mallards feeding on seeds is a non-linear type II curve (Fritz et al. 2001). Heterogeneity of the food distribution was generated by subdividing the tray in imaginary cells, which were filled with seeds (8.8 seeds/cm\(^2\)) or left empty (0 seeds/cm\(^2\)) in a chessboard pattern (Fig. 2a). Cell-size was varied between distributions to create different scales of heterogeneity. In this experiment distributions were used with cell-widths of 1.0, 2.0, 3.0 and 6.5 cm. To ensure seeds were cryptic to the mallards, the layer of food items was covered with another 0.5 cm thick layer of sediment. The tray was topped off with water.

To determine whether mallards respond to heterogeneity we measured the time devoted to filled and empty cells, unlike Kawata and Agawa (1999) who measured the speed at which animals were moving in filled and empty cells, which is a less direct trait. Because we could not see the (tip of) the bill as soon as the bill was inserted into the sediment we developed a system that automatically registered the position of the tip of the bill.

The system consisted of 121 magnet sensors, mounted in the bottom of the feeding tray in a regular array (11 x 11), with a distance between two sensors measuring 1.0 cm (Fig. 2a,c). The presence or absence of a magnet to all sensors was continuously monitored at a frequency of 10 s\(^{-1}\). Below the tip of the lower jaw of the bill we mounted a small magnet disc (Neodinium; diameter 9.0 mm, thickness 2.0 mm, mass 1.3 g; Northwest Magnet Inc. Oregon, USA) using pieces of waterproof adhesive tape (Leukoplast; Beiersdorf AG, Hamburg, Germany) (Fig. 2b). To ensure a firm attachment the tape was shortly moistened with di-ethyl-ether. After a trial the magnet and tape were removed with Aceton. The size of the magnet determined the maximum distance at which a sensor was activated. We used a magnet with a specific size, for which a sensor was activated as soon as the tip of the bill was in the sediment and not when the bill was outside the sediment. Occasionally two sensors were activated, presumably when the bill was inserted deeply into the sediment and the magnet was close to the bottom of the feeding tray.

Mallards were fasted for 12 h before each experimental trial. Just before a trial started a magnet was attached. Subsequently, the duck was placed in an experimental unit (cage of 1 x 1 x 1 m with layer of sand on the ground) where it was allowed to feed from the tray. One food distribution was offered to one individual duck per trail. We conducted one to four replicates per food distribution per individual duck. The order in which different food distributions were offered to the ducks was randomized per individual duck, to avoid that a duck would get habituated to a certain distribution. In total 14, 17, 18 and 15 successful
trials were collected for food distributions with a cell width of 1.0, 2.0, 3.0 and 6.5 cm respectively.

**Experiment B: Instantaneous intake rate**

For the same six individual mallards we determined the instantaneous intake rate on four differently scaled heterogeneous food distributions. In this experiment heterogeneous food distributions with a cell-width of 1.5, 2.1, 3.0 and 7.5 cm were used. The Perspex feeding tray used in this experiment measured 15 x 15 x 4 cm.

In theory the intake rate at a fine scaled heterogeneous food distribution equals the intake rate at a homogeneous distribution with an equal overall food density (i.e. in our case half of the food density of filled cells; 0.5 x 8.8 = 4.4 seeds/cm$^2$), because the forager reacts to a fine scaled heterogeneous distribution as if it is homogeneous, i.e. fully mixed (Kotliar and Wiens 1990). The predicted intake rate at a coarse scaled food distribution equals the intake rate at a homogeneous distribution with a food density equal to the density within a filled cell of the coarse scaled distribution (in our case 8.8 seeds/cm$^2$), if all foraging effort can be allocated to the filled cells. To investigate these predictions the instantaneous intake rate was also determined at two homogeneous food distributions with low (4.4 seeds/cm$^2$) or high (8.8 seeds/cm$^2$) food densities.

In order to avoid effects of food depletion, the feeding tray was removed after the mallard had fed approximately 30 s. Feeding trials were video-taped and analyzed using The Observer Video-Pro software (Noldus Information Technology, Wageningen, the Netherlands). We defined feeding time as the total time that the tip of the bill was below the water surface. After the trial remaining millet seeds were collected by pouring the sediment over a 1-mm sieve and weighted after drying for 12 hrs in a stove ($80 ^\circ$C). The number of remaining seeds was determined by dividing the weight by seed weight (determined by weighing 100 seeds). Instantaneous intake rate was calculated by dividing the total number of seeds eaten by the feeding time. Per trial one food distribution was offered to one individual duck. One to four replicates were conducted per food distribution per duck. The order in which different food distributions were offered to the ducks was randomized per individual duck, to avoid that a duck would get habituated to a certain distribution. In total 21, 23, 23 and 31 trials were successful for food distributions with a cell width of 1.5, 2.1, 3.0 and 7.5 cm respectively. 20 and 21 successful trials were collected for homogeneous food distributions with a low and high food density.

**Data analysis**

*Experiment A: Foraging scale*

From a complete registration only the first 150 recordings (equivalent to 15 s of foraging) were used in the analysis to avoid effects of foraging itself on the distribution of the food items, and hence on the reaction to the distribution. In the analyses we only used
information from sensors below a filled or an empty cell and not from sensors below cell borders (Fig. 2a,c).

If mallards do not respond to existing heterogeneity, the probability that a filled or an empty cell is visited is equal. The number of visits to filled cells can be described by a binomial distribution (p (and q) = 0.5), given the total number of magnet registrations. A minor correction was used for p and q when the total number of cells was uneven. For every trial we calculated the probability of the observed number of visits to filled cells based on the total number of visits (one tailed test using the probability density distribution of the corresponding binomial distribution). When P < 0.05 we concluded that mallards did react to the offered heterogeneity because significantly more time was spent in filled than in empty cells.

To get a general impression of the exploitation patterns we explored whether mallards searched systematically or randomly within a tray by calculating the rate at which the tray was exploited for the whole registration. The tray was divided into 121 cells (or sectors conform Price and Correll 2001), corresponding to the position of the magnet sensors (every sensor is placed in the middle of a 1x1 cm cell). The presence in a cell and movements between cells were recorded by the magnet sensors. The tip of the bill had moved to the next cell at the moment that the sensor related to the current cell was not activated anymore, and therefore the time of one move is variable. We described exploitation patterns by relating the cumulative number of cells entered at least once to the number of between-cell moves. Predictions of exploitation patterns for random and systematic search were calculated according to Price and Correll (2001). Because occasionally two cells were visited at the same time we included the average number of cells visited per move (A) in the calculations. For random search the expected number of cells E(X) that was visited at least ones after N moves was calculated by:

\[
E(X) = 121 - 121 \left( \frac{121 - A}{121} \right)^N
\]

For perfect systematic search E(X) was calculated by:

\[
E(X) = \begin{cases} 
AN & \text{if } AN \leq 121 \\
121 & \text{if } AN > 121 
\end{cases}
\]

To investigate if a foraging reward results in an area restricted search we calculated the displacement for five successive steps for search paths starting in a an empty or full cell (tray divided in 121 cells; every cell measures 1x1 cm and is situated above a magnet sensor). We assumed that mallards received a positive foraging reward if they were visiting
Figure 3  A. Cumulative time (s) allocated to the positions in a feeding tray as recorded by magnetic sensors during the first 15 s of sample trials on four food distributions differing in the scale of heterogeneity (from left to right cell-width of food distribution is 1.0, 2.0, 3.0 and 6.5 cm). B. Search patterns as recorded by magnet sensors of the same trials. C. Positions of filled and empty cells classified for the same trials for the different food distributions. Black: cell is filled with 8.8 seeds/cm², white: cell is empty.

Figure 4  Proportion of time allocated to filled (black) and empty (open) cells for all experimental trials for four food distributions, differing in the scale of heterogeneity (from left to right cell-width of distribution: 1.0, 2.0, 3.0 and 6.5 cm). Trials in which significantly more time was devoted to filled cells are indicated by an asterisk. Individual ducks (A-F) are indicated below bars (at each cell dimension at sequence of trails).
a full cell. The position of the bill tip was recorded by the magnet sensors and a step was defined as a change in the recorded position. Displacement was calculated as the beeline distance from the initial magnet sensor (Smith 1974). If mallards conduct an area restricted search we expect a smaller displacement when the initial cell of the search path was filled, and a larger displacement when the initial cell was empty. The effect of initial cell content, step number and individual on beeline distance was analysed by general linear modelling (General Liner Models module of STATISTICA software package version 5.5 (Statsoft 1999)), with initial cell content and individual as categorical factors (fixed and random respectively) and step number as a continuous factor. Log transformed beeline distances were used to meet model assumptions.

Experiment B: Instantaneous intake rate
Trials in which birds foraged less than 25 s or more than 35 s were excluded from the analysis to avoid an effect of total feeding time. The effect of food distribution and individual on instantaneous intake rate was analysed in a two-way ANOVA with individual as a random factor. A Tukey post hoc test (for unequal sample sizes) was used to identify the effect of food distribution on intake rate. Analyses were conducted using the STATISTICA software package version 5.5 (Statsoft 1999).

Results
Experiment A: Foraging scale
The foraging pattern of mallards matched the distribution of food items at food distributions with a cell-width of 3.0 and 6.5 cm (Fig. 3a). At these food distributions mallards spent significantly more time in filled than in empty cells (Fig. 4). Mallards clearly responded to heterogeneity and were able to concentrate foraging effort in profitable areas. At a food distribution with a cell-width of 2.0 cm it is difficult to conclude if the foraging pattern matched the distribution of food items (Fig. 3a). However in 7 out of 17 trials significant more time was spent in full than in empty cells (Fig. 4). At least in these trials mallards responded to heterogeneity and allocated foraging effort successfully to cells containing food items. The foraging pattern of mallards did not match the distribution of food items at the food distribution with a cell-width of 1.0 cm (Fig. 3a). Also the time devoted to filled and empty cells did not differ significantly (Fig. 4). At this scale mallards did not respond to heterogeneity and failed to concentrate foraging effort in profitable areas. We conclude that the foraging scale of mallard is in between a cell-width of 1.0 and 2.0 cm. We reason that the foraging scale is very close to a cell-width of 2.0 cm because at a food distribution with a cell-width of 2.0 cm mallards responded to heterogeneity in only 7 out of 17 trials.

Mallards revisited cells frequently during foraging at all food distributions (Fig. 3b). Observed exploitation patterns were below the pattern predicted for systematic search and matched the pattern predicted for random search (Fig. 5). We tested if observed exploration
patterns deviated from the pattern predicted for random search by comparing the amount of observations above and below the predicted number of cells visited at least once after 100 steps, in a one tailed test using the probability density distribution of a binomial distribution \((p=q=0.5)\). At the fine scaled food distribution (cell-width 1.0 cm) previously searched cells were revisited at a frequency as predicted for random search (Fig. 5) \((p=0.16)\). For the coarse scaled food distributions (cell-widths of 2.0, 3.0 and 6.5 cm) mallards made more revisits than predicted for random search, resulting in significantly lower values of the number of cells visited at least once at 100 steps \((p<0.001\) for all distributions).

The number of revisits increased with scale for the coarse scaled food distributions. After 100 steps fewer cells were visited with increasing scale of food distribution (Jonckheere-Terpstra test, \(J=414, p<0.001\)).

**Figure 5** Exploitation patterns of a feeding tray for four food distributions, differing in the scale of heterogeneity (cell-width of different distributions: A. 1.0 cm, B. 2.0 cm, C. 3.0 cm, D. 6.5 cm) for all experimental trials. Tray was divided in 121 cells (of 1 x 1 cm each). Movement between cells and present position was recorded by magnet sensors. Exploitation patterns predicted by *systematic* and *random* search are indicated by a thick dashed line and a thick curved and continuous line respectively.
foraging scale of tactile-foraging Mallard

Table 1 Results (F-values and significance levels: * P < 0.05, *** P < 0.001, NS: not significant) of General Linear Modelling, analysing the influence of individual, initial cell content and step number on beeline distance with initial cell content and individual as categorical factors (fixed and random respectively) and step number as a continuous factor, for food distributions with different cell-widths.

<table>
<thead>
<tr>
<th>Food distribution</th>
<th>Individual</th>
<th>Initial cell content</th>
<th>Step number</th>
<th>df error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>22.61***</td>
<td>4.77*</td>
<td>403.06***</td>
<td>745</td>
</tr>
<tr>
<td>2.0</td>
<td>4.65***</td>
<td>0.80NS</td>
<td>378.00***</td>
<td>744</td>
</tr>
<tr>
<td>3.0</td>
<td>44.36***</td>
<td>39.45***</td>
<td>388.22***</td>
<td>980</td>
</tr>
<tr>
<td>6.5</td>
<td>6.12***</td>
<td>26.72***</td>
<td>232.56***</td>
<td>494</td>
</tr>
</tbody>
</table>

Table 2 Results of a two-way ANOVA testing the influence of food distribution and individual on the instantaneous intake rate, with food distribution as a fixed and individual as a random factor.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1</td>
<td>71463.85</td>
<td>239.3480</td>
<td>0.000020</td>
</tr>
<tr>
<td>Individual</td>
<td>5</td>
<td>310.15</td>
<td>20.2056</td>
<td>0.000000</td>
</tr>
<tr>
<td>Food distribution</td>
<td>5</td>
<td>242.90</td>
<td>15.8242</td>
<td>0.000000</td>
</tr>
<tr>
<td>Residual</td>
<td>138</td>
<td>15.35</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3 Results (P-values) of Tukey post hoc test to identify the effect of food distribution on intake rate, as analysed in a two-way ANOVA with food distribution as a fixed and individual duck as a random factor. HE: Heterogeneous food distribution with a cell-width of 1.5, 2.1, 3.0 or 7.5 cm. HO: Homogeneous food distribution with a food density of 4.4 or 8.8 seeds/cm².

<table>
<thead>
<tr>
<th>HE 1.5</th>
<th>HE 2.1</th>
<th>HE 3.0</th>
<th>HE 7.5</th>
<th>HO 4.4</th>
</tr>
</thead>
<tbody>
<tr>
<td>HE 1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HE 2.1</td>
<td>0.0195</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HE 3.0</td>
<td>0.0002</td>
<td>0.7351</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HE 7.5</td>
<td>&lt; 0.0001</td>
<td>0.4329</td>
<td>0.9992</td>
<td></td>
</tr>
<tr>
<td>HO 4.4</td>
<td>0.6780</td>
<td>0.8003</td>
<td>0.1118</td>
<td>0.0465</td>
</tr>
<tr>
<td>HO 8.8</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>0.0029</td>
<td>0.0078</td>
</tr>
</tbody>
</table>
The content of the initial cell had a significant effect on the beeline distance for the food distributions with a cell-width of 3.0 and 6.5 cm (Table 1). For these distributions the displacement was larger if the initial cell did not contain food items and smaller if the initial cell did contain food items (Fig. 6). We conclude that mallards showed an area restricted search on these food distributions.

For the food distribution with a cell-width of 1.0 cm the initial cell content had a significant effect on beeline distance (Table 1), but the effect was opposite to our predictions (displacement was smaller if the initial cell was empty). For the food distribution with a cell-width of 2.0 cm no significant effect of initial cell content was found (Table 1), also not when we only considered the trials in which mallards responded to heterogeneity (separate GLM; F=0.06, P=0.80). We conclude that an area restricted search was not conducted on food distributions with a cell-width of 1.0 and 2.0 cm.

**Experiment B: Instantaneous intake rate**

Food distribution and individual had a significant effect on the instantaneous intake rate (Table 2). The intake rate at a fine scaled food distribution (cell-width 1.5 cm) was significantly lower than at the coarse scaled food distributions (cell-widths 2.1, 3.0 and 7.5 cm) (Fig. 7, Table 3).

As predicted the intake rate at the low density homogeneous food distribution (4.4 seeds/cm$^2$) was significantly lower than the intake rate at the coarse scaled food distribution with a cell-width of 7.5 cm. It did not differ from the intake rates at the other food distributions, although it tended to be significantly lower than the intake rate at the food distribution with a cell-width of 3.0 cm (Table 3). The intake rate at the homogeneous distribution seems to be intermediate to the intake rates of the fine scaled distribution and the coarse scaled distributions.

Mallards reached the highest intake rate at the homogeneous high density food distribution (8.8 seeds/cm$^2$), which was significantly different from the intake rates at all other food distributions.

**Discussion**

**Foraging scale**

In this research we successfully demonstrate that mallards have a foraging scale, defined as the scale above which foragers do respond and below which foragers do not respond to spatial heterogeneity. The foraging scale of mallard is small (slightly smaller than 2x 2 cm) and is probably related to the morphology of the bill tip (bill width 1.5 and 2.4 cm for lower and upper mandible respectively). The foraging scale of several other species is also related to the morphology of their foraging apparatus. Oystercatchers *Haemotopus ostralegus* for example probe for buried prey with a slightly opened bill, and a small area is sampled at every probe (0.15 cm$^2$). Assuming that prey are only detected by direct touch prey
Figure 6 Movement patterns at food distributions, differing in the scale of heterogeneity (cell-width A. 1.0 cm, B. 2.0 cm, C. 3.0 cm, D. 6.5 cm), for parts of foraging paths starting in a cell with food items (Full cell, filled circles, solid line) or in a cell without food items (Empty cell, empty circles, dashed line). Numbers refer to trials in each condition. Beeline distance is defined as the displacement from the starting point. Movements and present position were recorded by magnet sensors.

Figure 7 Instantaneous intake rate (± se) during the first 30 s for different food distributions. At the left (white panel) four heterogeneous food distributions differing in scale (from left to right the cell-width of the distributions is 1.5, 2.1, 3.0 and 7.5 cm respectively, as indicated below the figure) were on offer. In the grey panel (at right) two homogeneous food distributions are considered, differing in food density (left: 4.4 seeds per cm², equal to overall food density of heterogeneous distribution; right: 8.8 seeds per cm², equal to food density within a filled cell of a heterogeneous distribution). Above the figure the outcome of a Tukey post-hoc test is indicated (at the 0.05 level).
encounter rates can be explained when this foraging scale is taken into account (Hulscher 1982). Knots *Calidris canutus* also probe for buried prey, but in addition to direct touch, these birds are able to detect prey items from a distance, which results in a larger foraging scale or detection area (5.2-6.4 cm$^2$) (Piersma et al. 1998, Piersma et al. 1995). The foraging scale (bite size) of different herbivorous mammalian and avian species is also related to the size of the mouth/bill and scales with body mass (Durant et al. 2003, Shipley et al. 1994, Wilson and Kerley 2003). In contrast, the foraging scale of other species, for example freshwater snails *Physa acuta* (Kawata and Agawa 1999) and Bewick's swans *Cygnus columbianus bewickii* (Van Eerden et al. 1997), is larger than the body size. The large foraging scale of Bewick's swans is the result of specific foraging behaviour. Swans dig pits (~1m$^2$) in order to retrieve food items from the sediment. Clearly, foraging behaviour in addition to bill morphology seems to be a factor determining the foraging scale.

The foraging scale differs between species, and consequently the response to the environment. It has been suggested that differences in the foraging scale can be a mechanism behind the coexistence of different species (Fierer and Kotler 2000, Illius and Gordon 1987). This would also hold for Anseriform species regarding the large differences in bill morphology (see for example Kooloos et al. (1989)).

If the behaviour of a forager is related to the abundance of food it is important to describe the environment at the foraging scale, because the foraging scale determines the range of food densities a forager perceives. In several studies the scale at which food abundance is described is based on practical considerations instead of the foraging scale (for example Bautista et al. (1995), Ens and Goss-Custard (1984), Lovvorn and Gillingham (1996) and Piersma et al. (1993), with the exception of for example Nolet and Mooij (2002) and Wanink and Zwarts (2001)). However, if a forager is able to respond to heterogeneity within the sampling scale of the observer, the food density the forager responds to can differ from the food density the observer measured at that spot. Also when the carrying capacity is calculated it is important to describe the food abundance at the appropriate foraging scale (Pielou 1977). If food abundance is described at a larger scale the food stock is underestimated because small scale heterogeneity is ignored (like for example in Beekman et al. (1991)).

*Allocating foraging effort*

The ability to concentrate foraging efforts within areas with high food density is constrained by the scale of the food distribution, as shown in our research. At coarse scaled distributions mallards spent more time in filled than in empty cells, in contrast to fine scaled distributions, at which mallards failed to concentrate their effort. This difference is partly explained by the search mode because exploration patterns differ between fine and coarse scaled food distributions. At coarse scaled food distributions more cells are revisited during exploitation than predicted by random search patterns. The number of revisits increases with the scale
of the food distribution. A possible explanation for an increase of revisits is area restricted search (Benhamou 1992).

However, evidence for area restricted search was only found at food distributions with cell-widths of 3.0 and 6.5 cm. Interestingly, these food distributions are clumped distributions (filled foraging scales neighbour filled foraging scales and empty foraging scales neighbour empty foraging scales), whereas the other food distributions (cell-widths 2.0 and 1.0 cm) are a regular distribution (2.0 cm: filled foraging scales neighbour empty foraging scales and visa versa) or a homogeneous distribution (1.0 cm), if delimited at the foraging scale. We hypothesize that area restricted search is only conducted in clumped food distributions, where this behaviour may have an adaptive value for the forager (Benhamou 1992, Smith 1974).

Because mallards are able to concentrate foraging efforts within areas with high food density even without conducting an area restricted search (food distribution with cell-width of 2.0 cm), we conclude that micropatch partitioning by itself can be a mechanism that results in an appropriate response to heterogeneity. This would imply that mallards are able to assess the quality of individual spots within the tray (at the foraging scale), and use sampling information to decide on local residence times. A similar response rule in treating the environment is described by Arditi and Dacorogna (1988), who predict that foraging spots are depleted to a fixed giving up density. However, their hypothesis, though fascinating, is still not verified by empirical data.

**Benefit of a response to heterogeneity**

The instantaneous intake rate is significantly higher at heterogeneous food distributions where mallards are able to concentrate foraging effort in filled cells than at heterogeneous food distributions where mallards fail to do so. Hence under certain conditions Mallard profit from their ability to concentrate foraging effort within areas with high food density.

In this experiment mallards were not omniscient regarding the position of filled and empty cells, but had to sample the environment to assess the quality of a spot. As a result they could not perfectly address all their feeding efforts to filled cells because they have to search for them. This explains why the intake rate at the coarse scaled food distributions is lower than the intake rate at the homogenous food distribution with a high food density (in this experiment identical to the food density within a filled cell in the heterogeneous distributions).

Although differences were not significant in all comparisons, a strong trend exits that the intake rate at the homogeneous low-density food distribution is lower than the intake rate at the coarse scaled food distributions and is equal to the fine scaled distribution, according to our predictions. Therefore the mallard joins the ranks of studies where a forager benefits from spatial heterogeneity whenever it is able to respond to it (Sparrow 1999).
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