Prior knowledge about spatial pattern affects patch assessment rather than movement between patches in tactile-feeding mallard

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Summary

1. Heterogeneity in food abundance allows a forager to concentrate foraging effort in patches that are rich in food. This might be problematic when food is cryptic, as the content of patches is unknown prior to foraging. In such case knowledge about the spatial pattern in the distribution of food might be beneficial as this enables a forager to estimate the content of surrounding patches. A forager can benefit from this pre-harvest information about the food distribution by regulating time in patches and/or movement between patches.

2. We conducted an experiment with mallard *Anas platyrhynchos* foraging in environments with random, regular, and clumped spatial configurations of full and empty patches. An assessment model was used to predict the time in patches for different spatial distributions, in which a mallard is predicted to remain in a patch until its potential intake rate drops to the average intake rate that can be achieved in the environment. A movement model was used to predict lengths of interpatch movements for different spatial distributions, in which a mallard is predicted to travel to the patch where it expects the highest intake rate.

3. Consistent with predictions, in the clumped distribution mallard spent less time in an empty patch when the previously visited neighbouring patch had been empty than when it had been full. This effect was not observed for the random distribution. This shows that mallard use pre-harvest information on spatial pattern to improve patch assessment. Patch assessment could not be evaluated for the regular distribution.

4. Movements that started in an empty patch were longer than movements that started in a full patch. Contrary to model predictions this effect was observed for all spatial distributions, rather than for the clumped distribution only. In this experiment mallard did not regulate movement in relation to pattern.

5. An explanation for the result that pre-harvest information on spatial pattern affected patch assessment rather than movement is that mallard move to the nearest patch where the expected intake rate is higher than the critical value, rather than to the patch where the highest intake rate is expected.

Key-words: incomplete information, learning, marginal value theorem, optimal foraging theory, spatial arrangement.

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Introduction

Spatial heterogeneity in the abundance of food provides a forager an opportunity to enhance its food intake rate by concentrating foraging effort within profitable areas (Valone & Brown 1989). However, when food items are cryptic this might not be a simple task as the content of patches is not obvious prior to exploitation. We see a patch as a discrete spatial entity of the environment (e.g. a branch for a foraging woodpecker; Olsson *et al*. 1999) or as the spatial entity that is exploited during the time the forager does not move (e.g. the part of the field that is grazed without moving the front legs for an ungulate, also called a foraging station; Focardi, Marcellini & Montanaro 1996).

Basically, there are two ways in which a forager can realize a beneficial skew in the allocation of feeding effort: (1) by regulating the time in patches (Charnov 1976), and (2) by regulating movement between patches (Walsh 1996). Information about the food distribution is essential in order to regulate time and movement in the most profitable way (Dall *et al*. 2005). A forager can have access to different sources of information about the content of patches. First, a forager acquires information during patch exploitation. This is called 'patch sample information' and it typically includes the number of prey found and the time spent foraging (Valone 1991). Secondly, a forager may have acquired information about characteristics of the food distribution during earlier visits to the habitat. This prior knowledge is called pre-harvest information (Valone 1991). Finally, a forager can perceive information about the quality of patches by monitoring the foraging success of other foragers. This vicarious sampling of resource quality has been termed 'public information' (Valone & Templeton 2002).

In order to be able to regulate the time in the patch a forager in an environment with cryptic food densities has to assess (rather than 'knows') the quality of a patch (Oaten 1977). A faster assessment is beneficial to a forager as less time is devoted to poor patches and more time can be devoted to rich ones (Clark & Mangel 1986; Valone & Brown 1989). Patch assessment is enhanced by combining patch sample information with pre-harvest information, a process called Bayesian updating (Iwasa, Higashi & Yamamura 1981; Green 1984; Olsson & Holmgren 2000; Van Gils *et al*. 2003). In current Bayesian assessment models, the frequency distribution of food densities is considered to be pre-harvest information the forager has access to (Green 1984; Olsson *et al*. 1999; Van Gils *et al*. 2003). In these models, the probability that a certain food density is encountered is thus equal to the frequency in which this density occurs in the environment. The frequency distribution of food densities is related to spatial variation in the abundance of food. However, this so-called spatial variance is not the only characteristic of a heterogeneous food distribution (Li & Reynolds 1995; Wiens 2000), and consequently is not the only possible source of pre-

harvest information. Different food densities are usually not randomly distributed throughout the area, but spatial pattern exists (Li & Reynolds 1995; Wiens 2000). Spatial pattern implies that the probability to encounter a certain density in a nearby patch depends on the content of the current patch (Mangel & Adler 1994). For instance, in a clumped food configuration the probability that a high-density patch is encountered nearby is higher if the density in the current patch is high. Thus, knowledge about the content of a patch provides information about the content of nearby patches for a forager that knows the spatial distribution of food. The spatial distribution is thus another form of pre-harvest information, which can be used to improve patch assessment (Bayesian updating).

To efficiently regulate its movement, a forager, in an environment with cryptic food densities, should use pre-harvest information on the spatial pattern of the food distribution. A forager that is sensitive to spatial pattern can enhance its intake rate by regulating the length and/or direction of movements between patches to its recent foraging experience. For example, in a clumped food configuration a forager can enhance the encounter rate with high-density patches and avoid area with low-density patches by intensifying the search from a high-density patch (shorter movements, increased sinuosity; also called area-restricted search) and weaken search from a low-density patch (longer movements, decreased sinuosity) (Benhamou 1992; Klaassen *et al*. 2006).

We are aware of only one study in which an effect of spatial pattern is demonstrated on both patch assessment and movement pattern. Fortin (2003) described foraging behaviour of free ranging bison *Bos bison*. During winter, bison dig craters in the snow to reach vegetation. A crater is considered equal to a foraging patch. Movement between patches appears to be non-random and linked to the spatial pattern in vegetation, as suggested by the observation that poor patches are encountered less often than the proportion available. Moreover, it was shown that areas of similar food quality were searched with different intensities, which was explained by differences in recent foraging experiences. The latter result indicates that also the assessment of a patch was affected by spatial pattern in vegetation.

In the current study we explore whether pre-harvest information on spatial pattern affects patch assessment and/or movement patterns in tactile-foraging mallard *Anas platyrhynchos*. Qualitative theoretical predictions are tested in a laboratory experiment in which mallard were solitarily foraging in environments with random, clumped and regular spatial distributions of cryptic food densities (the frequency distribution was not varied). To the best of our knowledge, this study is the first experiment to assess the significance of pre-harvest information about the spatial distribution of food densities on both patch assessment and movement patterns, using contrasting spatial configurations of food densities.

Theoretical predictions

We here introduce two models to illustrate the effects we expect of spatial pattern on patch assessment and on movement pattern. Models provide predictions about assessment and movement for the specific food distributions used in the experiments. This includes a random, a clumped and a regular spatial configuration of full (20 wheat seeds buried in sediment) and empty (sediment only) patches. Note that here we use the terms 'random', 'clumped' and 'regular' to indicate different spatial distributions. The same vocabulary is often used for frequency distributions, such as the Poisson, negative binomial and binomial distribution. In our case, distributions do not differ in the frequency of full and empty patches, i.e. always half of the patches are full. We describe spatial pattern by so-called structure functions, as this describes spatial pattern from the forager's perspective (Mangel & Adler 1994). A structure function is the probability that a patch at distance *i* is full, given the state of the current patch (full or empty, Fig. 1). Further details about the food distribution are provided below.

Energy expenditures were not considered in the models. To make our point it appeared to be sufficient to derive (qualitative) predictions from gross intake rate estimates because, in this case, intake rate is predominantly affected by time rather than by energy.

PATCH ASSESSMENT MODEL

Seeds are often cryptic and buried in sediment, thus we assume that a forager is incapable of an instantaneous assessment of the content of a patch upon arrival (Valone & Brown 1989). A forager has a prior expectation about the content of a patch based on pre-harvest information. In a random food distribution spatial pattern contains no information, thus the prior expectation is solely based on pre-harvest information about the frequency distribution of food densities (i.e. spatial variance). In this case, the probability that a patch is full, upon arrival, is 0·5, irrespective of the content of the previous patch. In clumped and regular food configurations, there is spatial information, thus the prior expectation about the content of a patch is based on a combination of pre-harvest information about both the frequency
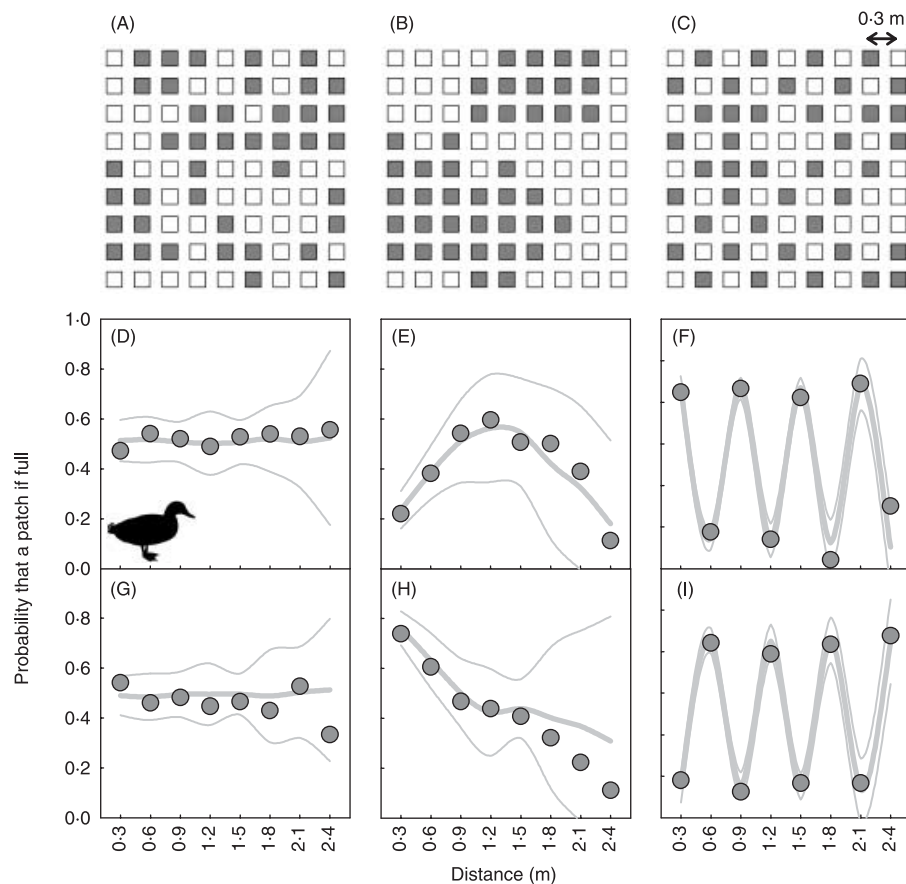
Fig. 1. Examples of a random (A), clumped (B) and regular (C) spatial configuration of full (grey squares) and empty (open squares) food trays. A tray represents a patch for a foraging mallard. A full patch contains 20 wheat seeds, an empty patch contains no seeds. Distance between the centres of neighbouring patches measures 0·3 m. (D–I) Structure functions, i.e. the probability that a patch at distance *i* from a current patch is full, given that the current patch is empty (upper row, D–F) or that the current patch is full (lower row, G–I). Dots correspond to structure functions for the particular configurations depicted in panels A–C. Grey lines depict average structure functions for the corresponding type of spatial distribution used in this study (thick line is average, thin lines are 95% confidence limits). (D,G) Random; (E,F) clumped; (F,I) regular distribution. Note that in this graph distances are categorized (dots).

and the spatial distribution of densities. In these cases, the probability that a patch is full depends on the content of the (adjacent) previously visited patch, as described by the structure functions (see Fig. 1). For example, for the clumped configuration considered in this study, the probability that a patch is full is 0·76 if the adjacent patch was full and 0·24 if the adjacent patch was empty.

During exploitation the expectation about the content of a patch is continuously updated with patch sample information (Iwasa *et al.* 1981). In our experiment we only have two patch types (empty and full), thus when a forager finds one food item it instantaneously knows that it is in a full patch. It is consequently most interesting to examine how the expectation about the content of a patch develops over time as long as no prey is found. The (posterior) probability that a patch is full (Po_F) as a function of time in the patch (t), when no food items are found is (after Olsson 2006):

$$Po_F(t) = \frac{P_F \cdot e^{-20At}}{1 - P_F + P_F \cdot e^{-20At}} \qquad \text{eqn 1}$$

where P_F is the (prior) probability that the patch is full at $t = 0$ (i.e. upon arrival in the patch) and A is the search efficiency ($A = 0·04$ patch s^{-1}, based on the type II functional response with handling time $t_h = 0·65$ s, as observed in this study). P_F can be derived from the structure function. The expectation that a patch is full, given the incident that no food items are found, decreases over time (Fig. 2). This decrease is more pronounced for the clumped configuration when the previous patch was empty and the regular configuration when the previous patch was full, which is the result of lower P_F's (Fig. 2).

As pointed out by Green (1984), Olsson & Holmgren (1998) and Olsson & Brown (2006) an assessing forager maximizes its long-term intake rate by leaving a patch as soon as the expected potential intake rate during the remainder of the patch visit drops to a certain critical intake rate C. In order to predict the time a forager spends in an empty patch (patch residence time, PRT), we calculated the potential intake rate over time in a patch from the posterior probability that the patch is full, according to Olsson (2006). As we are interested in the effect of pre-harvest information about spatial pattern on patch assessment we calculated the potential intake rate over time for the situation that the previous (neighbouring) patch had been empty (posterior distribution for previous empty patch) and for the situation that the previous patch had been full (posterior distribution for previous full patch). The critical intake rate that maximizes long-term intake rate is different for these situations (except for the random distribution), because these situations represent different environments. We took the average of these critical intake rates as the critical intake rate for the specific spatial distribution, and calculated the potential intake rate over time for the previous patch being empty and for the previous patch being full, for this average critical intake
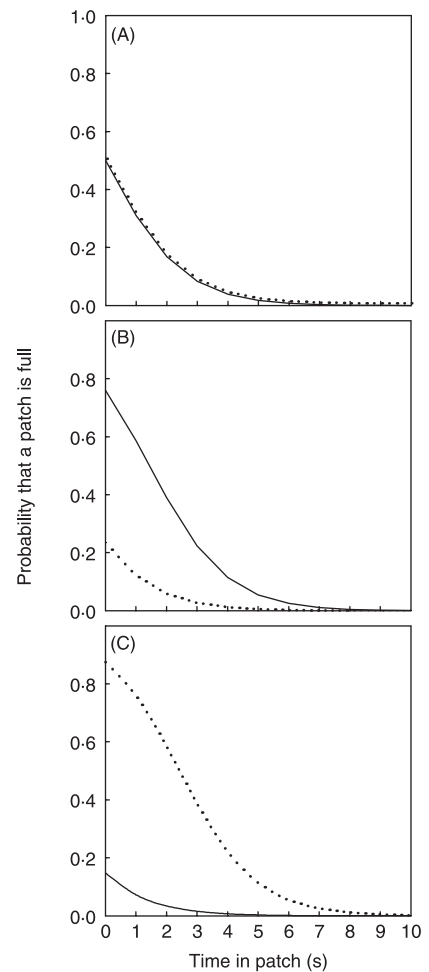
Fig. 2. Probability that a patch is full over time in the patch as long as no food item is found, if the previous (neighbouring) patch had been full (solid line) or empty (dotted line). (A) Random, (B) clumped and (C) regular spatial configuration of full and empty patches throughout the environment.

rate. The critical intake rate was 0·24 for the random distribution, 0·26 for the regular distribution, and 0·25 for the clumped distribution. We checked for each spatial distribution that the intake rate that was achieved by the modelled forager was equal to the specific critical intake rate (results not shown).

For clumped and regular distributions, the time after which the estimate of the potential intake rate reaches the critical level C depends on the content of the previous patch (Fig. 3). Consequently, we predict that the time that a forager spends in an empty patch depends on the content of the previous adjacent patch in the clumped and regular, and not in the random distribution. In particular, for the clumped configuration we predict that the PRT in an empty patch is longer if the previous patch had been full than if the previous patch had been empty. In contrast, for the regular configuration we predict that the PRT in an empty patch is longer if the previous patch had been empty than if the previous patch had been full. For the random configuration we predict no differences in PRTs if the previous patch had been full or empty.
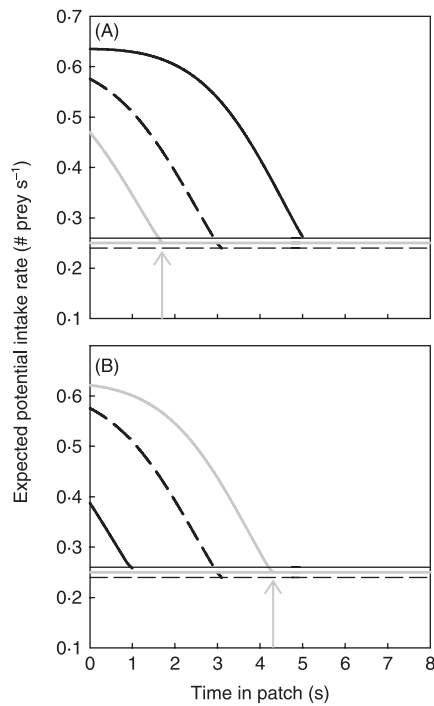
Fig. 3. The expected potential intake rate in a patch over time, as long as no food item is found, if the previous (neighbouring) patch had been empty (A) or full (B). The dashed line corresponds to a random configuration, the grey solid line to a clumped configuration, and the black solid line to a regular configuration of full and empty patches. Horizontal lines depict the critical intake rates at which a forager is predicted to leave a patch (dashed line for random, grey line for clumped, and solid line for regular configuration). The grey arrow indicates the time after which a forager is predicted to leave a patch for the clumped food configuration; about 1·7 s when the previous patch had been empty, and about 4·3 s when previous patch had been full.

INTERPATCH MOVEMENT MODEL

In order to evaluate the optimal movement between patches we calculated the expected gross intake rate over distance (see also Klaassen *et al.* 2006). The probability that a patch at distance i is full, given the content of the current patch, is described by the structure functions (Mangel & Adler 1994). Mallard consumed on average nine seeds in a full patch (this study), thus we can calculate the expected gross intake $\hat{n}$ in a patch at distance i, given the content of the current patch b (b can be full (F) or empty (E)), by:

$$\hat{n}(i) \mid b = P(F_i \mid b) \cdot 9 + P(E_i \mid b) \cdot 0 \qquad \text{eqn 2}$$

which equals:

$$\hat{n}(i) \mid b = P(F_i \mid b) \cdot 9 \qquad \text{eqn 3}$$

where $P(F_i \mid b)$ and $P(E_i \mid b)$ stand for the probability that a patch at distance i is full (F) or empty (E), respectively, conditioned on the content of the current patch, as given by the structure function.

The expected time $\hat{t}$ to travel to and spend in a patch at distance i, given the content of the current patch, is correspondingly calculated by:

$$\hat{t}(i) \mid b = P(F_i \mid b) \cdot \left(t_F + \frac{i}{v} \right) + P(E_i \mid b) \cdot \left(t_E + \frac{i}{v} \right) \qquad \text{eqn 4}$$

where t_F is the time foraging in a full patch (11·22 s, this study), t_E is the time foraging in an empty patch (2·33 s, this study), and v is the velocity of a mallard (0·25 m s^{-1}, this study).

Subsequently, we can calculate the expected gross intake rate $\hat{N}$ in a patch at distance i, given the content of the current patch by dividing the expected gross intake by the expected time:

$$\hat{N}(i) \mid b = \frac{\hat{n}(i) \mid b}{\hat{t}(i) \mid b} \qquad \text{eqn 5}$$

The intake rate that a mallard should expect in a patch at distance i is affected by the content of the current patch in clumped and regular but not in random configurations (Fig. 4). For the random configuration the highest intake rate is always expected in the adjacent patch (Fig. 4). For the clumped configuration the highest intake rate is expected in the adjacent patch if the current patch is full and in a more distant patch if the current patch is empty (Fig. 4). For the regular configuration the highest intake rate is expected in the adjacent patch if the current patch is empty and in a more distant patch if the current patch is full (Fig. 4). Thus a mallard that moves to the patch where the highest intake rate is expected, is predicted to always move to the adjacent patch in the random configuration, to the adjacent patch if the current patch is full and to a distant patch if the current patch is empty for a clumped configuration, and to the adjacent patch if the current patch is empty and to a distant patch if the current patch is full for a regular configuration (Fig. 4).

Experiments

FOOD DISTRIBUTION

Food was distributed over 81 plastic trays ($12 \times 12 \times 6$ cm), placed in a 9×9 array (30 cm between centres of two adjacent trays; examples in Fig. 1; a tray is treated as a foraging patch for a mallard). All trays were filled with a 4 cm layer of coarse-grained sand, and water was added until the water level equalled the level of sand. In half of the trays 20 wheat seeds per tray were buried in the sediment. We checked by visual inspection that seeds did not protrude the sediment in order to ensure that seeds were cryptic to the mallard.

We created food distributions with random, clumped and regular spatial configurations of full and empty trays, by selectively positioning full and empty trays throughout the array. In a random configuration no spatial relationships exist. In a clumped configuration, a positive spatial autocorrelation exists, whereas in a regular configuration a negative spatial autocorrelation exists (Legendre 1993). Spatial pattern was quantitatively described by Moran's *I*, a measure of spatial
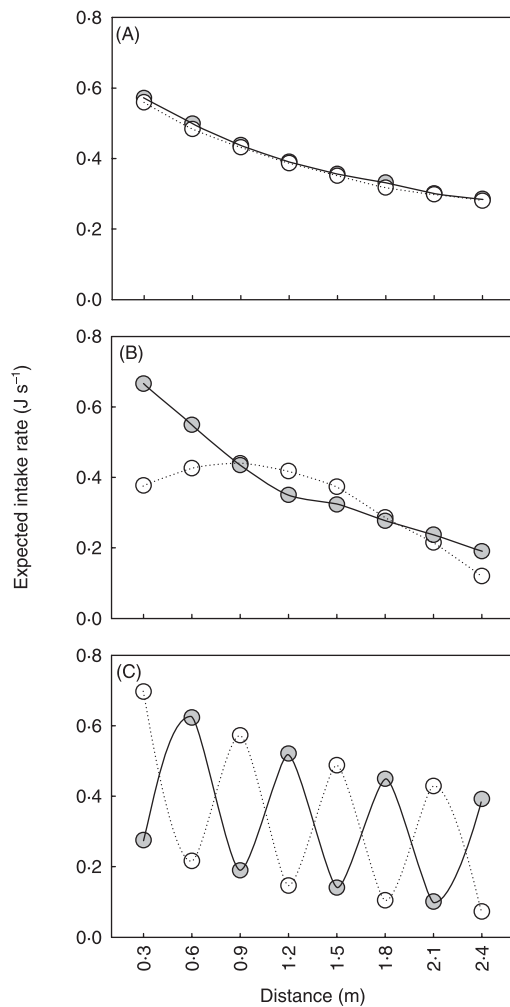
Fig. 4. The gross intake rate that is expected in a patch at distance *i* from the current patch, given that the current patch is empty (open symbols) or that the current patch is full (grey symbols). Different panels relate to different spatial distributions of full and empty patches: (A) random, (B) clumped and (C) regular configuration. Lines and symbols overlap for the random configuration. For the random configuration the highest intake rate is always expected in the neighbouring patch. For the clumped configuration the highest intake rate is expected in the neighbouring patch when the current patch is full, and in the third patch ($i = 0.9$) when the current patch is empty. For the regular configuration the highest intake rate is expected in the neighbouring patch when the current patch is empty, and in the second patch ($i = 0.6$) when the current patch is full.

autocorrelation, under the randomization hypothesis using the Rookcase add-in, with adjacency defined as Rook's (Sawada 1999). No significant spatial autocorrelations could be detected for the random configurations (average Moran's I index of 0·4, average $P = 0·24$). Spatial autocorrelation was highly significant for all clumped and regular configurations (average Moran's I index of 6·5 and −8·4, respectively, all $P < 0·01$).

Moreover, spatial pattern was described from the perspective of the forager by structure functions (Fig. 1, and Mangel & Adler 1994). Structure functions differed dramatically for different types of spatial

distributions (Fig. 1). For random configurations, the probability that a patch was full was about 0·5 for all distances, irrespective the content of the current patch. For clumped configurations, the probability that a patch was full decreased over distance if the current patch was full and increased and subsequently decreased over distance if the current patch was empty (Fig. 1). Structure functions for regular configurations strongly fluctuate (Fig. 1).

EXPERIMENTAL TRIALS

Experimental trials were conducted from 7 to 26 March 2005 with eight mallard (four males, four females). Between trials, mallard were kept in an outside aviary where food (mixture of grains and pellets) was provided after experimental trials for a period of 1 h. Ducks were feeding solitarily and one trial was performed per duck per day.

Food was offered in the same spatial distribution (random, clumped or regular) to a duck for 6 successive days. After 1 day without a trial, another type of spatial distribution was offered to the same individual duck for another six successive days. Again, after 1 day without a trial, the remaining spatial distribution was offered to the same duck for another six successive days. The order in which different types of spatial distributions were offered to individual ducks was according to a random block design. Configurations with the same spatial distribution differed in the exact position of full and empty patches to avoid that ducks could learn the position of full patches. The structure function of a particular configuration always fell within the 95% confidence limits around the average structure function for that specific distribution (determined by excluding the focal configuration, like in a cross-validation, see Fig. 1).

A trial was started at the moment that the duck was released into the experimental room. During a trial a duck was continuously observed from a separate room through a one-way mirror. The order in which food trays were visited was recorded. Furthermore, the whole trial was recorded by a video system. After a duck visited 50 patches or after a period of 15 min, whichever was the shortest, a trial was ended. After a trial trays were collected, and the content of all full trays that were visited by the bird was sieved in order to determine the number of seeds eaten (per tray).

ANALYSES

Video captures were analysed using The Observer Video-Pro software (Noldus Information Technology, Wageningen, the Netherlands), in which media files were played back at half speed. From these captures we determined for every tray the time feeding in the tray (defined as the time having the tip of the bill below the sediment surface) and the length of the movements to the next tray (defined as the distance between the

centres of the current and the next visited tray). Furthermore, for every trial we calculated the gross intake rate the duck achieved by dividing the total number of seeds eaten by the total time feeding and moving.

We restricted the data analyses to the last experimental day of a week (we assume that ducks had learned characteristics of the spatial distribution by this day). Cases related to revisits of patches and cases related to full patches where less than two seeds were eaten were excluded. For the analysis of feeding time in empty patches, we only included cases where the previous and the current patch were adjacent (i.e. 0·3 m between centres of trays). The feeding time in an empty patch was analysed as a function of the food distribution and whether the previous patch was full or empty by general linear modelling (GLM), with 'content of the previous patch' (F or E), 'spatial distribution' (random, clumped or regular) and 'individual duck' as factors. Time in a patch was log transformed to meet model assumptions.

The length of a movement to the next patch, given the spatial pattern of the food distribution and the content of the patch where this movement was started was analysed by GLM, with 'content of the previous patch' (F or E), 'spatial distribution' (random, clumped or regular) and 'individual duck' as factors. Movement lengths were log transformed to meet model assumptions.

The average gross intake rate as a function of the food distribution was analysed by an factorial ANOVA, with 'spatial distribution' (random, clumped or regular) and 'individual duck' as factors.

All analyses were conducted using STATISTICA software package version 7·1 (StatSoft 2005).

Results

We obtained enough data for the random and clumped distribution for seven ducks. Data for one female duck were discarded because accidentally a regular instead of a clumped configuration was offered on the fourth day. Naturally, we did not obtain enough data for the regular distribution about the time that ducks spend in empty patches after a visit to an adjacent empty patch due to the fact that such a combination hardly occurs in this distribution. PRTs in empty patches were very different for different individual ducks ($F_{6,194} = 4·8$, $P < 0·01$, Fig. 5). More importantly, in a clumped environment all ducks spent more time in an empty patch if the previous patch was full than if the previous patch was empty ($F_{1,82} = 6·6$, $P = 0·01$, Fig. 5A). In a random environment no such effect of the content of a previous patch could be detected ($F_{1,112} = 0·9$, $P = 0·35$, Fig. 5B).

There was considerably less variation in the length of movements between ducks (no effect of individual: $F_{6,834} = 0·5$, $P = 0·80$), which is probably caused by the fact that almost all movements (96·3%) were to neighbouring patches. However, the length of a movement to the next patch was significantly affected by the content of the previous patch ($F_{1,834} = 7·4$, $P < 0·01$) and by type of spatial distribution ($F_{2,834} = 4·7$, $P < 0·01$), but
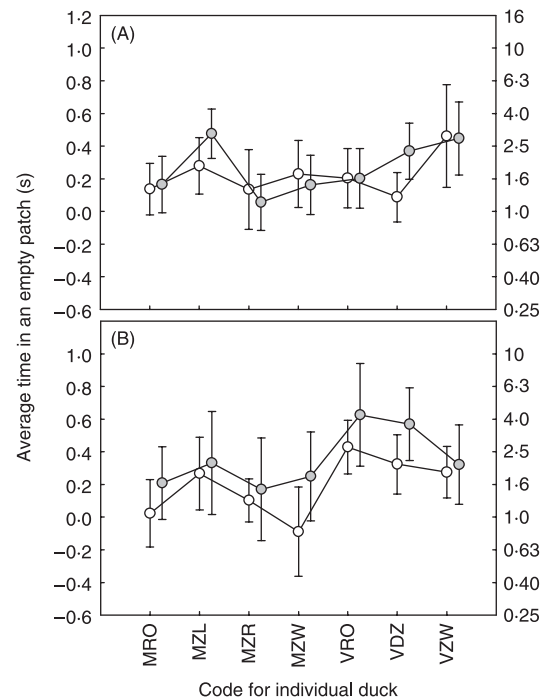
Fig. 5. The average time that a mallard spent in an empty patch after a visit to a neighbouring patch that had been full (filled circles) or that had been empty (open circles) (log-transformed values on left, untransformed values on right axis). Panel A corresponds to an environment with a random and panel B to an environment with a clumped spatial distribution of full and empty patches. Error bars denote 95% confidence limits.
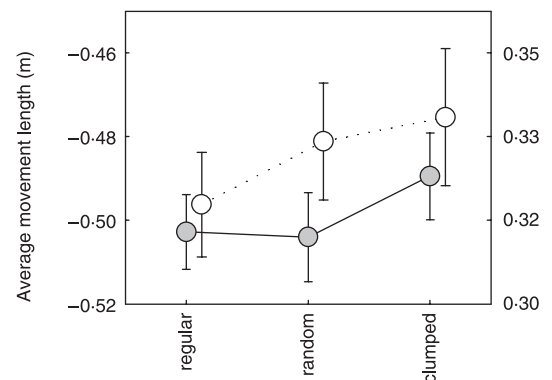
Fig. 6. The average length of movements that started in a full patch (grey dots) and or that started in an empty patch (white dots) (log-transformed values on left, untransformed values on right axis), for environments with a regular, random or clumped spatial distribution of full and empty patches. Error bars denote 95% confidence limits.

the effect of content of a previous patch was not different for different spatial patterns (interaction $F_{2,834} = 0·8$, $P = 0·45$). For all spatial distributions ducks tended to make larger movements from empty than from full patches, and the average length of a movement was largest in clumped and smallest in regular distributions (Fig. 6).

Finally, type of spatial distribution had a significant effect on the average intake rate ($F_{2,12} = 4·1$, $P = 0·04$).

A Tukey post-hoc test revealed that the intake rate in clumped configurations (average 0·43 seeds s⁻¹) was significantly higher than in regular configurations (average 0·33 seeds s⁻¹; $P = 0·04$), and a strong trend existed that it was also higher than in random configurations (average 0·34 seeds s⁻¹; $P = 0·05$).

Discussion

PATCH ASSESSMENT AND MOVEMENT PATTERN

In accordance to our predictions, mallard spent less time in an empty patch when the previous (neighbouring) patch had been empty than when the previous patch had been full, in environments with a clumped configuration of food. Such regulation of foraging time was not observed for environments with a random configuration of food densities. Unfortunately, due to the very nature of regular configurations we could not evaluate whether mallard regulated the time in patches in environments with a regular distribution of food densities. Nevertheless, mallard appeared to be sensitive to spatial pattern in the distribution of food densities, and used this pre-harvest information in their assessment of the content of patches.

There was no consistent agreement between prediction and observation for the length of movements between patches. As predicted for the clumped distribution, a movement that started in an empty patch was larger than a movement that started in a full patch, but a similar response was also observed in the other two spatial distributions where this response was not predicted. It appeared that mallard in all distributions almost always moved to a neighbouring patch (96·3%).

We conclude that the mallard in this experiment had learned the spatial pattern in the distribution of food densities, but that this knowledge only affected the assessment of patches and not the movement pattern between patches (at least not according to the predictions). An enhanced assessment seems to be linked to a higher intake rate.

CONDITIONS FOR REGULATING INTERPATCH MOVEMENT

In this study mallard responded to spatial pattern by regulating the time in patches rather than by regulating the movement between patches. In other studies a clear effect of spatial pattern on movement pattern was recorded (e.g. Smith 1974; Pienkowski 1983; Nolet & Mooij 2002; Fortin 2003; Klaassen, Nolet & Bankert 2006), which raises the question why movement is regulated in some and not in other cases.

Obviously, one condition for regulating movement in response to spatial pattern is that the spatial pattern is nonrandom. An example of a random food distribution is the distribution of winter buds of *Vallisneria americana* as fed on by canvasbacks *Aythya valisineria*
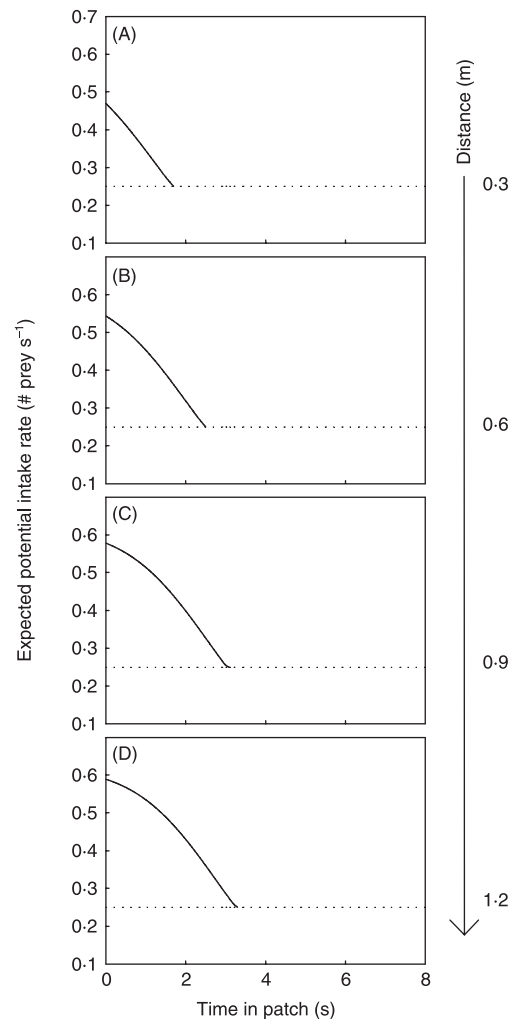
Fig. 7. The expected potential intake rate in a patch over time, as long as no food item is found, given that the previous patch had been empty, for an environment with a clumped distribution of full and empty patches. Different panels correspond to different distances from the previous patch, increasing from A (0·3 m, neighbouring patch) to D (1·2 m, fourth patch). The horizontal dotted line indicates the critical intake rate (which maximizes the long-term intake rate, 0·25 prey s⁻¹) at which patches are left. Note that for all these patches the expected intake rate upon arrival in a patch is above the critical intake rate.

(Lovvorn & Gillingham 1996). However, random configurations seem to be the exception rather than the rule, thus in most natural situations there seems to be an opportunity to fine-tune movement.

One possible explanation why mallard did not regulate movement in this study is that they do not travel to the patch where the highest intake rate is expected, but to the nearest patch where the expected intake rate upon arrival is higher than the critical intake rate. For example in the clumped distribution, the expected intake rate upon arrival in a patch was always higher than the critical intake rate, even when the adjacent patch had been empty (Fig. 7). It would consequently be interesting to determine movement patterns of mallard in an environment in which the expected intake

rate upon arrival in a patch is sometimes lower that the critical intake rate, to see whether mallard skip these patches.

The optimal patch-leaving behaviour is different for solitarily and social foragers. In a group the best tactic is to 'catch as catch can', i.e. to deplete patches down to the *current* average intake rate rather than down to the final *quitting* intake rate (Nolet, Klaassen & Mooij 2006). In analogy with these results we might expect that a forager in a group moves to the patch where the highest intake rate is expected (i.e. is sometimes skipping patches), rather than to the nearest patch where the expected intake rate is higher than the quitting intake rate. Interestingly, in all examples where an effect of pattern on movement was observed (see above) the foragers were most probably under exploitative competition, whereas the mallard in our experiment were feeding solitarily. An appealing follow-up experiment would thus be to establish movement patterns for mallard that are under exploitative competition, i.e. that are foraging in a group.

INTERACTION BETWEEN ASSESSMENT AND MOVEMENT MODELS

Traditional 'patch assessment models' assume no spatial pattern in the distribution of food densities (random spatial distribution) (Iwasa *et al.* 1981; Green 1984; Olsson *et al.* 1999; Van Gils *et al.* 2003; Olsson 2006). However, most natural food distributions are spatially patterned, and this spatial pattern could be another source of pre-harvest information about the content of patches. Hence, a spatially explicit version of patch assessment models, as introduced in this paper, is important to derive more realistic predictions of PRTs.

One other way to model the interaction between assessment and spatial pattern is used in 'movement velocity models' (Knoppien & Reddingius 1985; Krakauer & Rodriguez-Girones 1995). These models assume that foragers move in lines, in which the time spent at a point along this line (and consequently the searching efficiency, cf. Gendron & Staddon 1983) is inversely related to the velocity of movement. An adaptive response to spatial pattern is realized by adjusting the velocity of movement to the recent foraging experience. In essence, these models thus predict the time at a patch (each point along the line can be considered as a patch, Kacelnik & Bernstein 1988), given the content of the current patch, and the spatial pattern of the environment.

In 'patch assessment' and 'movement velocity' models, foragers encounter food densities in proportion to their availability. However, a forager that moves strategically through a spatially patterned environment encounters low-density patches less often and high-density patches more often than the proportions in which these patches occur. Basically there are two ways to move 'strategically': (1) by regulating the sinuosity of the foraging path ('two-dimensional movement models'; Benhamou 1992; Hill, Burrows & Hughes 2003), and (2) by regulating

the length of movements between patches ('discrete movement models'; Klaassen *et al.* 2006; Klaassen *et al.* 2006). A strategically moving forager perceives a richer environment, and is consequently expected to leave patches at a higher critical intake rate. To calculate the optimal critical intake rate in such a case, one should thus correct for the biased encounter of rich patches.

In our experiment mallard did not regulate the sinuosity of their path (frequency distribution of turning angles was equal for movements from empty and from full patches, $\chi^2_7 < 0.20$, $P > 0.98$ for all distributions). In fact, mallard moved in straight lines and only made turns when approaching the edge of the food distribution. Mallard did also not regulate the length of movements between patches (see Results). Hence, in our case the optimal critical intake rate was simply the average critical intake rate for the situations that the previous patch had been full or empty (see Experiments).

The abovementioned models find their application in specific situations, and it seems that there is no general model that grasps all the possible ways in which a forager can respond to spatial variance and spatial pattern in the abundance of food. It is now the challenge to understand why foragers regulate particular aspects in certain but not in other circumstances. This not only needs a detailed review of the different ways different types of foragers respond to spatial heterogeneity, but also detailed experiments that tackle specific questions, similar to this study.

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