The use of a flexible patch leaving rule under exploitative competition: a field test with swans

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Bart Nolet taking one of the 1584 sediment cores that made up the basic sampling scheme. Arnaud Elger is sieving a previous sample.
Abstract

Learning animals are predicted to use a flexible patch-leaving threshold (PLT) while foraging in a depletable environment under exploitative competition. This prediction was tested in flock-feeding Bewick’s swans (Cygnus columbianus bewickii) depleting hidden tubers of fennel pondweed (Potamogeton pectinatus) in a two-dimensional, continuous environment. The swans’ patch residence time was measured by combining recordings of the foraging behaviour and movement paths. The tuber biomass density was measured before and after the period of exploitation, using the presumable foraging window of the swans as the scale of measurement. Swan foraging was simulated in order to predict the effects of flexible and fixed PLTs, respectively, on the patch residence time and the spatial heterogeneity of the tuber biomass density. Flexible PLTs were predicted to lead to short and decreasing patch residence times and a decrease in the coefficient of variation in tuber biomass densities, whereas the reverse was generally the case for fixed PLTs. Observed patch residence times did not decrease with time and were intermediate between those predicted for swans with flexible and fixed PLTs. Furthermore, an increase of the coefficient of variation in the tuber biomass density was observed. Given the observed giving-up biomass densities the most likely model was one with swans with a fixed rather than a flexible PLT. These results point at factors that may affect the spacing behaviour or constrain the use of a flexible PLT in swans.
Introduction
The study of foraging in a spatially heterogeneous environment has progressed by gradually incorporating more and more realism into the models. In the classical model of Charnov (1976), a solitary forager moves successively between equidistant, discrete patches. It assumes no patch re-visitation and random search within patches, with prey captures being so frequent that it can be described as a continuous, deterministic process. The model predicts that the forager should leave a patch when the current intake rate in the patch drops to the average intake rate for the habitat. This has become known as the marginal value theorem. Provided that the functional response is the same in all patches, a forager is thus predicted to equalise resource densities among visited patches (with higher initial resource densities than the giving-up density).

The notion of discrete patches may be realistic in some settings, for example flowers in a meadow visited by nectar-feeding insects or trees visited by larvae-eating woodpeckers. However, in many environments such as the savannah grazed by antelopes, patches cannot be distinguished a priori. Theory predicts however that animals partition such continuous environments in parts with a food density above or below a critical threshold, thus creating their own food patches (Arditi and Dacorogna 1988). The parts with higher initial food densities should be grazed down to the critical density. In this way, the effect of the forager on the remaining biomass density will be similar to the situation with discrete patches.

The above models deal with animals foraging alone, but the optimal patch-leaving behaviour may be different when competitors are around, in particular when there is interference. When competitors do not interfere with each other, the gain rate of animals that stay in the patch does not increase after one of the other animals in the patch has left. This implies that all individuals should leave at the time predicted by the marginal value theorem (Sjerps and Haccou 1994, Haccou et al. 1999). Still, under exploitative competition, so when competitors are competing for access to patches varying in quality, the best tactic is presumably to "catch as catch can", in analogy with optimal prey choice under these circumstances. Considering diet choice between two prey types, a solitary forager is predicted to either always accept only the best prey or to always accept both prey types, regardless of the level of depletion, whereas under exploitative competition the predator is predicted to switch from accepting only the best prey to accepting both prey types during the process of depletion (Mitchell 1990, Visser 1991). Analogously, when competitors are simultaneously depleting the environment, the best patch-leaving tactic is to deplete patches down to the current average intake rate of the environment rather than down to the final quitting intake rate. Partly exploited patches are later revisited, so in effect patches are predicted to be depleted in a few visits in succession.

Bernstein et al. (1988) applied this tactic of animals using a marginal value like patch-leaving threshold (PLT) when modelling depletion under exploitative competition. The foragers instantly knew their capture rate and hence the quality of the local patch, but...
learnt the quality of the environment as a whole, and left patches as soon as their current intake rate fell below the intake rate expected for the environment. Because the environment changed due to depletion, their PLT also changed and was thus flexible. Several studies have used this model as a basis, investigating the effects of model assumptions on the distribution of foragers relative to the distribution of the resources (Beauchamp et al. 1997, Tyler and Hargrove 1997, Ward et al. 2000). To our knowledge, no study has yet tested the prediction of the model that animals use a flexible PLT while foraging in a depletable environment under exploitative competition. Our objective was to test this prediction.

The study system consisted of Bewick's swans (Cygnus columbianus bewickii) feeding on fennel pondweed (Potamogeton pectinatus). In temperate regions, fennel pondweed is a pseudo-annual, which reproduces mainly asexually by means of below-ground tubers (Van Wijk 1988). Bewick's swans preferably feed on these tubers during migration (Beekman et al. 1991, Nolet et al. 2001a). At the time of swan foraging, the above-ground plant matter has been washed away, so no visual clues are present to guide the swans, and patches are not identifiable as such. However, the swans dig pits by trampling with their feet and by doing so create their own food patches (Brouwer and Tinbergen 1939, Beekman et al. 1991). The size of these pits is c. 1 m² (Van Eerden et al. 1997). Swans forage in flocks, and defend their pits against other swans (Van Eerden et al. 1997), but otherwise interference is not apparent (Nolet et al. 2002). The mortality of tubers from other causes than swan foraging is negligible during the short period (2-4 weeks) of swan exploitation (Jonzén et al. 2002). After exploitation of the pondweed beds, the swans switch to harvest leftovers of sugar beets on the surrounding fields (Beekman et al. 1991).

Our study system is thus a typical example of one in which foragers with learning capabilities are foraging under exploitative competition in a two-dimensional, continuous environment with hidden prey. Prey items are very small compared to the consumer (biomass ratio in the order of 1:50 000), and the resource intake can be described as a continuous, deterministic process. The study system further has a hierarchical patch structure with exclusive access to small patches (pits) within a pondweed bed, and a shared, large patch in the form of the pondweed bed. The PLTs were studied at the pit-level, assuming a fixed PLT at the bed-level (Nolet et al. 2002). Swan foraging was simulated based on previous work (Nolet et al. 2002, Nolet et al. 2001b, Nolet and Mooij 2002), contrasting two patch-leaving rules at the pit-level: a fixed and a flexible PLT. Foragers with a fixed PLT grazed down each part of the habitat until their energy gain dropped to a fixed critical level. In contrast, foragers with a flexible PLT grazed down each part to the current estimate of the critical energy gain, readjusting their PLT during depletion of the habitat. An invasibility analysis confirmed that as expected foragers with a flexible PLT were superior to foragers with a fixed PLT.
In order to test whether swans use a flexible PLT, simulation models that assumed either a fixed or flexible PLT were confronted with field data on swan foraging and tuber depletion. Firstly, residence time in foraging pits was predicted to be longer and more constant for swans using a fixed PLT than for swans using a flexible PLT, for which it was predicted to be shorter and to decrease with resource depletion. Secondly, the coefficient of variation in the prey density biomass was predicted to increase or decrease depending on whether swans used a fixed or flexible PLT, respectively.

Methods

Study area
The field study was performed in the Lauwersmeer (53°22’ N, 06°13’ E; the Netherlands) in an area closed to the public (the Babbelaar). The Lauwersmeer is a shallow freshwater lake (2000 ha) of which the parts <0.7 m deep are largely covered with fennel pondweed (total coverage c. 270 ha). The lake is an important stopover of Bewick’s swans during their autumn migration (Beekman et al. 1991).

Swan foraging behaviour
Foraging behaviour of Bewick’s swans was observed in October 2001. Observations were made during day-light hours from one of two small hides on the bank at the edge of the pondweed bed. Movement pattern and foraging behaviour of a focal swan were simultaneously recorded until the swan stopped foraging or the distance between the hide and the swan exceeded 100 m (the range of the measuring device). Every time a focal swan submerged its head, the angle and distance to the swan was measured using a total station range-finder (reflectorless type TCR307, Leica Geosystems BV, Rijswijk, the Netherlands). The behaviour was classified (trampling, head-dipping, up-ending, surfacing, swimming, various non-foraging behaviours, see Nolet et al. 2001b) and recorded on a handheld microcomputer (Organiser II Model LZ64, Psion plc, London, UK) using The Observer software (Noldus Information Technology, Wageningen, the Netherlands). The behaviour was grouped into foraging bouts, one bout consisting of one sequence of trampling, underwater feeding (head-dipping and/or up-ending), and surfacing.

In one foraging pit, more than one foraging bout can take place. In order to determine pit residence times, the movement pattern between foraging bouts was analysed in terms of step lengths l (the distance between two subsequent foraging bouts) and net distance moved D_i (sometimes termed net displacement, i.e. the linear distance between the location of the initial foraging bout and the foraging bout i steps later) (Turchin 1998). The frequency distribution of all recorded log-transformed step lengths was bi-modal. The fit of a mixture of two normal distributions with a probability density of q \cdot N(l, \mu_1, \sigma_1) + (1 - q) \cdot N(l, \mu_2, \sigma_2), where q is a constant between 0 and 1, and N is the normal distribution with mean \mu and standard deviation \sigma was compared with that of a single normal distribution.
Taking the difference between the number of estimated parameters into account, the bi-modal distribution fitted significantly better than the uni-modal one according to the log-likelihood ratio test (Sokal and Rohlf 1995): $\chi^2 = 133, p < 0.0001$. The bi-modal distribution was subsequently split at the intersection of the two comprising distributions (back-transformed $l^* = 0.62$ m). For the left part (the small step lengths), the average observed net distance moved was smaller than the size of a foraging pit ($1 \text{ m}^2$) up to at least 19 subsequent steps (average $D_{19} = 0.25$ m). In contrast, for the right part (the large step lengths), the average net movement was larger than the size of a foraging pit already after 1 step (average $D_1 = 5.1$ m). Thus, based on the step length between foraging bouts, the foraging behaviour of swans was split into feeding inside a pit ($l < l^*$) and searching between pits ($l > l^*$). For pits for which both the start and end of the pit visit were recorded, the number of subsequent foraging bouts per pit and the total underwater feeding time per pit (Pit Residence Time PRT) were determined. Data were averaged per focal swan.

Swan exploitation of the 10×10 m grid sampled for tubers (see Tuber depletion pattern) was recorded by four automatic photo-cameras around the grid, yielding a total of 2-3 pictures per day between 5 October and 19 November 2001.

**Tuber depletion pattern**

Tubers were sampled by taking sediment cores which were washed through a 3-mm sieve, and the tubers were subsequently dried for a minimum of 48 h at 70 °C. First, the maximum tuber burial depth was determined by extracting 40 cm sediment, which was sliced into 5 cm parts. In a total of 192 cores (7 cm in diameter) no tubers were found below 35 cm. Based on this finding, at least 35 cm deep cores (10 cm in diameter) were used in the remaining sampling programme.

Tuber biomass density was measured in quadrats of 1 m$^2$. In order to obtain an estimate of the variance within a quadrat, the tubers were collected per quarter quadrat (0.25 m$^2$). The number of cores taken was a compromise between the accuracy of the estimate of the tuber biomass density (which should be great) and the area sampled (which should be small because of destructive sampling). In order to determine the accuracy of the estimate, a 100×100×60-cm high frame with 8×8 cells was pushed 40 cm deep into the sediment. Hereby it was possible to take cores close together, one core per cell, extracting half of the sediment in the cell. The tubers were weighed per core. It was subsequently determined how the estimate of the tuber biomass density was dependent on the number of cores. From each quarter quadrat, a core result was randomly drawn (without replacement), and after each complete draw (i.e., from all four quarter quadrats) the percent absolute deviation of the current average from the grand average (i.e. of the 64 cores) was calculated. This procedure was repeated 100 times. Based on the results, 3 cores were taken per quarter quadrat (equivalent to 12 cores per quadrat), yielding a median absolute
deviation of 12.8% of the actual tuber biomass density in the quadrat by sampling 9.4% of the area.

Sampling was performed at two scales. First, 100 quadrats in a grid of 10×10 m were sampled (1200 cores in total). This grid was marked with poles placed 12 m apart. Second, 33 quadrats were sampled (396 cores in total) in a lattice pattern with quadrats 20 m apart over an area of 60×200 m. This inter-quadrat distance was chosen because tuber biomass densities ≥20 m apart can be regarded as independent (Nolet and Mooij 2002). The sampling site was sandy and shallow. The water depth, which was measured relative to the usual water level in October (-83 cm, expressed relative to the Netherlands’ standard), varied in space between 40 and 47 cm.

Sampling took place in the first week of October 2001 (before the swans arrived) and mid-November 2001 (after the period of swan exploitation). Both the tuber biomass densities before and after swan grazing were ln-transformed, and unbiased estimates of the (proportional) variance among and within quadrats were obtained by ANOVA (Sokal and Rohlf 1995: 215). As a measure of spatial autocorrelation in tuber biomass density, Moran’s I was calculated under the randomisation hypothesis using the Rookcase add-in, with adjacency defined as Queen’s (considering the four cardinal plus four diagonal neighbouring cells) (Sawada 1999).

Model
In order to predict the pit residence times and the depletion patterns for the two contrasting PLT tactics, swan exploitation was simulated with an individual-based foraging model, described in detail in Nolet and Mooij (2002).

The pondweed bed was modelled as a grid consisting of 40×40 cells. The cell size of the grid (1 m²) was equal to the size of a foraging pit. This was assumed to be equal to the foraging window of the swans (Kotliar and Wiens 1990); in other words, the swans were assumed not to respond to variation in biomass density within a cell. A focal part of 10×10 cells contained the same initial biomass densities as observed in the field grid (28.9 g m⁻² ± 12.1 SD, n = 100), after correction for the tubers extracted during the sampling in early October (i.e., multiplied by 1-12 π 0.05²) (Fig. 2a). The distribution of tuber biomass densities of the lattice sampling did not differ significantly from normal (30.6 g m⁻² ± 12.2 SD, n = 33, Kolmogorov D = 0.1242, p > 0.1). Thus, in the remaining 10×10 m parts of the virtual grid the tuber biomass densities were distributed in the same spatial configuration as in the field grid, but scaled to an average tuber biomass density drawn from a normal distribution with the same mean and standard deviation as the lattice sampling data.

Under exploitative competition, 16 swans were simultaneously introduced to 16 randomly picked cells on the 40×40 m grid, simulating peak densities (0.01 birds m⁻²) observed in the field. The grid had wrap-around margins so that a swan swimming out of
the grid on one side reappeared on the opposite side. This represents foraging on a large pondweed bed and in a large flock.

The model swans foraged in bouts consisting of a fixed sequence of trampling, underwater feeding and surfacing. The duration of the underwater feeding phase was calculated based on optimal use of oxygen over the foraging bout as described by Nolet et al. (2001b). The swans had perfect knowledge of the cell quality after one foraging bout, but learnt the quality of the whole bed, which constantly changed due to the depletion by the swans. Learning was modelled by a linear operator model which has been demonstrated to perform well in various contexts in comparison to other learning rules (Beauchamp 2000). In the linear operator model outdated information is devaluated at a rate depending on the memory factor $\mu$ (Bernstein et al. 1988):

$$\gamma_{x+1} = \mu \times g_x + (1-\mu)\gamma_x$$

where $\gamma$ is the expected gain rate, and $g$ is the actual gain rate. The gain is the net energy intake, so the gross energy intake minus all energetic costs. The time step $x$ was 1 s.

The model swans differed in the rules they used to decide to leave or stay in a cell. Swans had either a flexible or a fixed PLT at this cell level. A swan with a flexible PLT swam to another cell when the gain rate that it expected to obtain in the next foraging bout (of $n$ time steps) in the current cell was less than its current expected gain rate for the bed as a whole, so when:

$$\sum_{i=x+1}^{x+n} g_i \frac{1}{n} < \gamma_x$$

While swimming to another cell, all model swans alternated between extensive, directional search and intensive, random search, depending on whether they had decided to leave the current cell after one foraging bout or not (Nolet and Mooij 2002). Only one swan per cell was allowed, so patches were not shared at the cell level. This introduces some interference at the bed level, but this effect was small because only 1 in 100 moves were hampered by the presence of other swans in which case another optional cell was chosen. The swans entered the pondweed bed with an a priori expectation $\gamma_{prior}$ equal to the gain rate achievable on 30 g m$^{-2}$, and flew away (to an alternative habitat, i.e. a sugar beet field) as soon as the expected gain rate for the bed as a whole was less than its $\gamma_{GU}$:

$$\gamma_x < \gamma_{GU}$$
Table 1 Parameter values of the simulation model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Unit</th>
<th>Ref</th>
</tr>
</thead>
<tbody>
<tr>
<td>Assimilation of tubers (a)</td>
<td>0.90</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Energy density of tubers (e)</td>
<td>16.9</td>
<td>kJ g⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Handling time (t_h)</td>
<td>1.82</td>
<td>s g⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Attack rate (a)</td>
<td>0.00102</td>
<td>m² s⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Exponent of depletion (θ)</td>
<td>0.83</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Duration of trampling phase (τ)</td>
<td>1</td>
<td>s</td>
<td>1</td>
</tr>
<tr>
<td>Duration of recovery phase (s)</td>
<td>2</td>
<td>s</td>
<td>1</td>
</tr>
<tr>
<td>Duration of feeding phase (t)</td>
<td>5-12</td>
<td>s</td>
<td>1</td>
</tr>
<tr>
<td>Duration of swimming phase (-)</td>
<td>2¹, 14⁵</td>
<td>s</td>
<td>2</td>
</tr>
<tr>
<td>Metabolic rate during trampling² (m₁)</td>
<td>50.9</td>
<td>J s⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Metabolic rate during feeding³ (m₂)</td>
<td>27.4</td>
<td>J s⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Metabolic rate during recovery⁴ (m₃)</td>
<td>30.8</td>
<td>J s⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Metabolic rate during swimming⁵ (-)</td>
<td>28.2</td>
<td>J s⁻¹</td>
<td>3</td>
</tr>
<tr>
<td>Oxygen storage capacity (K)</td>
<td>180</td>
<td>ml O₂</td>
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</tr>
<tr>
<td>Exponent of oxygen replenishment (α)</td>
<td>0.5</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Prior expected gain rate (γGU)</td>
<td>243.7</td>
<td>J s⁻¹</td>
<td>4</td>
</tr>
</tbody>
</table>

Reference: (1) Nolet et al. (2001), (2) Nolet & Mooij (2002), (3) Nolet et al. (2002), (4) This study

As used in referred publication

Optimised (see text); ¹in intensive mode; ⁵in extensive mode; ²calculated assuming 20.0 J mlO₂⁻²

The model was parameterised using field and laboratory data collected in previous years (Nolet et al. 2002, Nolet et al. 2001, Nolet and Mooij 2002) (Table 1). The memory factor μ and the giving-up gain rate γGU are unknown, but a model swan had a given combination of μ (varying between 0.1 and 0.001) and γGU (expressed in tuber biomass densities varying between 3 and 11 g m⁻²).

During sampling in the field the boundaries of swan pits could not be reliably distinguished. As a result, after swan foraging a quadrat in the field may, in contrast to a cell in the model, consist of a combination of a grazed and non-grazed part. In order to account for this, the boundaries of the model cells were afterwards shifted one half cell length to the right and one half cell length downwards (shifting was performed in these directions as the boundary cells of the focal part of the grid had neighbouring cells to the right and/or below). Summing the biomasses in the four quarter cells that make up the shifted cell without accounting for the within-cell variation would lead to a considerable reduction in the between-cell variance. Therefore tuber biomass in the shifted cells B'ᵢⱼ was calculated as:

\[ B'ᵢⱼ = u₁ (0,0.5) Bᵢⱼ + u₂ (0,0.5) Bᵢⱼ+₁ + u₃ (0,0.5) Bᵢ+₁ⱼ + u₄ (0,0.5) Bᵢ+₁ⱼ+₁ \]

83
where \( u_1(0,0.5) \) \( \ldots \) \( u_4(0,0.5) \) are numbers drawn from a uniform distribution between 0 and 0.5, so that each of the four donating cells contributed on average 25% of the biomass. By applying it to the ungrazed situation it was confirmed that this procedure retained between-cell variance while not affecting the mean.

For each scenario (i.e., swans having one of the two contrasting PLT tactics and a given \( \mu, \gamma_{GU} \)-combination) the depletion of the model pondweed bed was obtained by simulating exploitation of the model pondweed bed by 16 identical swans until all swans had left the bed. After applying the shift described above to obtain grazed and ungrazed parts within model cells, the degree of agreement between these modelled final tuber biomass densities and the observed ones were measured with the log-likelihood ratio test (Sokal and Rohlf 1995). For this analysis the final tuber biomass densities (g/m\(^2\)) were again ln-transformed and classified in six classes (<1.6, 1.6-2.0, 2.0-2.4, 2.4-2.8, 2.8-3.2, >3.2). Because two parameters were used to calibrate the model (\( \mu \) and \( \gamma_{GU} \)), the test had 6 - 2 - 1 = 3 degrees of freedom.

In addition, the performances of swans with different PLT tactics were compared by investigating the exploitation with and without exploitative competition. First, one swan at the time was introduced in the model grid and gain curves of these solitarily foraging swans were obtained for both PLT tactics. Second, a game analogous to an invasibility analysis was simulated. One invader with the one PLT tactic was foraging simultaneously on the model pondweed bed with 15 residents with the alternative PLT tactic. Swans with a fixed of flexible PLT either had the same \( \mu \) and \( \gamma_{GU} \), or those specific \( \mu, \gamma_{GU} \)-combinations that yielded the maximum likelihoods as described above.

**Figure 1** Observed and predicted pit residence time PRT against total time spent foraging and swimming by Bewick’s swans on a pondweed bed. Observed PRTs (from two hides; dots) were intermediate between those predicted (mean ± 1 SD) according to the best-fitting scenarios for swans using a flexible or fixed patch-leaving threshold, respectively (lines).
**Results**

Swan exploitation

Swans were present in the Babbelaar from 18 to 24 October. During this exploitation period the swans were recorded in the direct neighbourhood of the field grid by the automatic cameras on two days (18 and 19 October 2001), with on average $1.0 \pm 0.7$ SE ($n = 4$) swans photographed whilst inside the poles (equivalent to $0.007 \pm 0.005$ swans m$^{-2}$). On four subsequent days swans were visible on the photographs foraging elsewhere on the pondweed bed, with high water levels being noted on one of these days. Swans were directly observed foraging in front of hide A on 18 to 20 October, and in front of hide B on 20, 23 and 24 October. On the photographs swans were recorded standing on the shore on 24 October, suggesting the depletion of the pondweed bed. On the next day the water level rose again and the swans disappeared.

The results from the direct observations of the foraging behaviour of the swans did not differ per hide (hide effect on mean pit residence time PRT: $t_{14} = -1.37, p > 0.1$; hide effect in ANCOVA of PRT with co-variable foraging and swimming time after accounting for one day of interruption at hide B due to high water levels: $F_{1,13} = 0.91, p > 0.3$). The data of the two hides were therefore pooled. The number of bouts per pit was $22 \pm 11$ (mean $\pm$ SD, $n = 16$ swans) and the pit residence time PRT was $273 \pm 147$ s (Fig. 1). PRT did not decrease significantly over time (the slope $B$ of the linear regression was not significantly different from zero (and positive): $72.7 \pm 46.2$ s/d ($B \pm$ SE), $t_{14} = 1.57, p > 0.1$).

In order to be able to compare the observed PRTs with predicted ones, we determined for both swan types the $\mu, \gamma_{GU}$-combination that yielded the best-fitting tuber depletion pattern (see Tuber depletion pattern). For these most-likely $\mu, \gamma_{GU}$-combinations, the observed PRTs were shorter than those predicted for swans using a fixed PLT, and longer than those predicted for swans using a flexible PLT (Fig. 1). Interestingly, the latter did not show the expected decrease in PRT in the course of exploitation (as opposed to swans using a flexible PLT with the same $\gamma_{GU}$ but smaller $\mu$; not shown) because these model swans had left the pondweed bed before a decrease in PRT became apparent (Fig. 1). The observed foraging and swimming time on a bed (i.e., clock time multiplied by 0.7 to account for 70% of the time spent foraging and swimming; B.A. Nolet and M. Klaassen, submitted) was with 1.9 to 2.5 days closer to that predicted for swans with a fixed PLT (1.7 days) than for swans with a flexible PLT (1.0 days) (Fig. 1).

**Tuber depletion pattern**

The spatial pattern in tubers revealed that there was a weak but highly significant positive autocorrelation in tuber biomass densities before swan grazing (Fig. 2a; Moran’s I = 0.125, $p < 0.005$). The average ln-transformed tuber biomass density was 3.175 (back-transformed 23.9 g m$^{-2}$) and the variance 0.191. After swan grazing the spatial autocorrelation had disappeared (Fig. 2b; Moran’s I = -0.035, $P > 0.3$). The average
been reduced to 2.492 (back-transformed 12.1 g m\(^{-2}\)), but the variance had increased to 0.362. Both the variance within and among quadrats roughly doubled due to the swan grazing, a highly significant change (Table 2).

![Figure 2](image-url) **Figure 2** Observed and modelled (ln-transformed) pondweed tuber biomass density in 10\(\times\)10 m grid (in both cases as part of a larger pondweed bed). (a) Observed before grazing by Bewick's swans, corrected for extracted tuber biomass during sampling. (b) Observed after swan grazing. (c) Predicted after grazing by swans using a flexible patch-leaving threshold (PLT) (according to the best-fitting scenario among those for swans with a flexible PLT: with swans with a memory factor \(\mu = 0.01\) and giving-up gain rate \(\gamma_{GU}\), expressed as tuber biomass density, \(\gamma = 11\) g m\(^{-2}\)). (d) Predicted after grazing by swans with fixed PLT (according to the most likely scenario: with swans with \(\mu = 0.005\) and \(\gamma_{GU} = 5\) g m\(^{-2}\)).

**Table 2** Unbiased estimates of the variance in ln-transformed tuber biomass density among and within quadrats (1 m\(^2\)), both before and after swan grazing, calculated using ANOVA. \(p_1\) gives the significance level of the test for differences among quadrats, and \(p_2\) gives the significance level of the test for differences in the variance before and after swan grazing. The results indicate that there is spatial heterogeneity in tuber biomass density in the field grid both before and after swan grazing (\(p_1\)), and that the coefficient of variation has significantly increased due to swan grazing (\(p_2\)).

<table>
<thead>
<tr>
<th>Formula</th>
<th>Before</th>
<th>After</th>
<th>(F_{99,99})</th>
<th>(p_2)</th>
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</thead>
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<tr>
<td>Among (\text{Var}<em>{\text{among}} = (\text{MS}</em>{\text{among}} - \text{MS}_{\text{within}})/n)</td>
<td>0.111</td>
<td>0.207</td>
<td>1.871</td>
<td>0.001</td>
</tr>
<tr>
<td>Within (\text{Var}<em>{\text{within}} = \text{MS}</em>{\text{within}})</td>
<td>0.776</td>
<td>1.809</td>
<td>2.331</td>
<td>0.0002</td>
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<tr>
<td>(F_{99,300})</td>
<td>1.571</td>
<td>1.458</td>
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<td>(p_1)</td>
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<td>0.008</td>
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</tbody>
</table>
Model swans were predicted to graze down the pondweed bed to the observed average (ln-transformed) tuber biomass density over a whole range of $\mu, \gamma_{GU}$-combinations, with $\mu$ and $\gamma_{GU}$ in the right combination being inversely related (Fig. 3a,c). This held for both swans with a flexible and a fixed PLT. When swans used a flexible PLT the variance however always decreased relative to the initial variance (Fig. 3b), whereas the variance increased when swans used a fixed PLT (provided that not all cells were grazed; Fig. 3d). When swans used a fixed PLT both the average and variance of the prediction were in accord with the observation in a small parameter space, i.e. for swans with $\mu = 0.005$ and $\gamma_{GU} = 5 \text{ g m}^{-2}$ (in tuber biomass density equivalents). This was also the most likely scenario given the observed giving-up biomass densities, i.e. the scenario with the smallest log-likelihood ratio $G$ ($G = 18.9$). The best-fitting scenario among those for swans using a flexible PLT was that for swans with $\mu = 0.01$ and $\gamma_{GU} = 11 \text{ g m}^{-2}$, but the fit to the observed data ($G = 38.8$) was
significantly less ($\chi^2 = 19.9, p < 0.0001$) than that of the most likely scenario (i.e., swans using a fixed PLT with $\mu = 0.005$ and $\gamma_{GU} = 5 \text{ g m}^{-2}$).

These best-fitting scenarios among those for swans using a fixed and flexible PLT, respectively, still yielded significant differences with the observed giving-up biomass densities ($\chi^2 = 18.9, p < 0.001$, and $\chi^2 = 38.8, p < 0.0001$, respectively) (Fig. 4). Swans with a fixed PLT were predicted to either graze cells down to a low biomass density or to leave them untouched, leading to a platykurtic frequency distribution, whereas swans with a flexible PLT grazed down many cells to intermediate biomass densities, leading to a leptokurtic frequency distribution. The observed frequency distribution was in between these extremes (cf. also Fig. 2b with 2c-d).

Swan game
In order to test whether a flexible PLT was indeed superior to a fixed PLT under exploitative competition, the performances of the two foraging tactics were compared.

First, the swans only differed in their patch-leaving rule, and not in their $\mu$ and $\gamma_{GU}$. While foraging alone, swans with a flexible PLT achieved a higher final cumulative gain than swans with a fixed PLT (Fig. 5a). This difference was due to the early departure from the pondweed bed by swans with a fixed PLT, which was in turn due to the greater fluctuations in their expected gain rate (Fig. 5b). The cumulative gain would have been the same if swans with a fixed PLT would have stayed in the pondweed bed as long as the swans with a flexible PLT (because swans with a flexible PLT attained a greater rate of gain than swans

![Figure 4](image-url) Frequency distribution of final ln-transformed tuber biomass densities per m$^2$, observed in a 10 $\times$ 10 m grid and predicted according to the best-fitting scenarios for swans using a flexible or fixed patch-leaving threshold, respectively. The distribution is either more leptokurtic (for flexible PLT) or platykurtic (for fixed PLT) than observed.
with a fixed PLT in the first half of their stay but a lower rate of gain in the second half). As a consequence of this asymmetrical gain rate, swans with a flexible PLT also achieved a higher gain than swans with a fixed PLT in the game (Fig. 6a,b). Particularly as invaders they benefited from the low performance of the residents with a fixed PLT early in the exploitation (Fig. 6b).

Figure 5 Comparison of the gain of swans using a flexible or fixed patch-leaving threshold (PLT) while foraging solitarily on a pondweed bed. (a) Cumulative gain of swans. The slope of the thin solid line is equal to the $\gamma_{ou}$ and the dashed line is the extrapolated linear regression through the data for swans with a fixed PLT. (b) Expected gain rate. Upper lines are the averages and lower lines the minima (number of swans > 7) of 15 simulations. The swans leave the pondweed bed when the expected gain rates fall below $\gamma_{ou}$ (the thin solid line). If the bed would be effectively depleted until the tuber biomass at which the gain rate is $\gamma_{ou}$, no difference in cumulative gain would exist between swans with a flexible or fixed PLT, but swans with a fixed PLT leave the bed prematurely due to the larger fluctuations in their expected gain rate. Memory factor $\mu = 0.005$ and giving-up gain rate $\gamma_{ou}$ (expressed as tuber biomass density) = 5 g m$^{-2}$.
Second, the swans were allowed to differ in their $\mu$ and $\gamma_{GU}$ (those belonging to the best-fitting scenarios for swans with a fixed and flexible PLT, respectively; Fig. 6c,d). In that case, swans with a flexible PLT still performed better despite their early departure from the pondweed bed due to their relatively high $\gamma_{GU}$; the lead taken at the pondweed bed was largely or even fully retained after their switch to the less profitable alternative habitat (arable land with harvest remains of sugar beets).

**Figure 6** Comparison of the gain of swans using a flexible or fixed patch-leaving threshold (PLT) while foraging simultaneously on a pondweed bed with one invader among 15 residents. Given are the average and SD (error bars) (number of swans > 7) of one simulation with 15 residents, and of 15 simulations with one invader (marked with asterisk). Swans with a flexible PLT gain more energy than swans with a fixed PLT, both (a,b) when they have the same memory factor ($\mu = 0.005$) as well as giving-up gain rate ($\gamma_{GU} = 5 \text{ g m}^{-2}$), and (c,d) when they have $\mu$s and $\gamma_{GU}$s according to their best-fitting scenarios (for flexible PLT $\mu = 0.01$ and $\gamma_{GU} = 11 \text{ g m}^{-2}$, and for fixed PLT $\mu = 0.005$ and $\gamma_{GU} = 5 \text{ g m}^{-2}$). The dashed lines indicate the gain in the alternative habitat (sugar beet fields), where the observed gain rate is equivalent to that at a tuber biomass density of 14 g/m$^2$ (see Fig. 5 in Nolet et al. 2002).
Discussion
Our model swans updated their expected gain rate every time step. Because pit residence time (PRT) varied with pit quality, this means that not every pit was weighted equally. The swans therefore did not build up an expectation of the habitat quality as such, but rather an expectation of the gain they could achieve in that habitat (accounting for their strategy to stay longer in rich pits than in poor ones). The expected rate of gain at the moment of pit initiation was a correct reflection of the past history of the actual gain rates. Because the memory factor determined the rate at which the expected gain rate was adjusted after a change in actual gain rate, pit residence time was inversely related to the memory factor. For swans with a flexible pit leaving threshold (PLT) the expected rate of gain at the moment of pit initiation decreased in the course of the habitat exploitation (as did average pit quality), whereas for swans with a fixed PLT the expected rate of gain at the moment of pit initiation (and therefore PRT) remained fairly constant (as did average non-grazed pit quality; grazed pits were left nearly instantaneously).

The game analysis confirmed that a flexible PLT would perform better than a fixed PLT under exploitative competition, also in our specific situation. The swans with a flexible PLT were better in exploiting the rich patches in the first half of the exploitation. Swans with a fixed PLT could generally not make up for this back-log during the second half of the exploitation because the rich patches had been partly depleted then. In addition, swans with a fixed PLT had often already left the pondweed bed by then. For a given combination of memory factor and giving-up threshold, swans with a fixed PLT tended to stay shorter at the model pondweed bed than swans with a flexible PLT because the former were more susceptible to a series of bad luck. Swans with a fixed PLT stayed long in cells that they accepted and consequently moved little, whereas swans with a flexible PLT tended to stay short in a cell and moved a lot between cells. As a result swans with a flexible PLT built up a more or less correct estimate of the gain achievable in the habitat, which decreased in time due to the depletion. In contrast, the expectation of swans with a fixed PLT fluctuated more strongly but did, on average, not change much, apart from the fluctuations increasing with time in the habitat. Since the model swans left the habitat as soon as the expected gain dropped below a giving-up gain, this happened, after a few runs of bad luck, much sooner in swans with a fixed PLT than in swans with a flexible PLT (provided they did not differ in memory factor and giving-up gain rate).

Contrary to our expectation, the observations were not consistent with the use of a flexible PLT. Simulations with swans with either a fixed or flexible PLT revealed that use of a fixed PLT was more likely given the observed giving-up biomass densities. In fact, use of a flexible PLT could be falsified because it predicted a decrease in the coefficient of variation in tuber biomass density whereas an increase (i.e., a doubling of the variance on the log-transformed scale) was observed (Table 2). However, although the data were more in accord with the use of a fixed PLT, the most likely scenario still did not explain the data very
well. In particular, the fixed PLT tactic predicted a too broad (i.e., platykurtic) frequency distribution of giving-up tuber biomass densities (Fig. 4). In fact, the observed frequency distribution was in between those predicted by the fixed and flexible PLTs. Similarly, the observed PRT was in between those predicted by the two PLTs (Fig. 1).

The question arises why swans would not use the best tactic, a flexible PLT, under exploitative competition. First, however, we have to consider the possibility that the swans were using a flexible PLT, but that the model failed to correctly predict their behaviour and consequent depletion patterns because of incorrect assumptions or overlooked constraints.

Competitors were assumed to be equal and behave independently, but this may not be the case. Earlier work with swans already revealed that differences in competitive ability between adult and subadult birds cause the subadult birds to exploit a poorer patch (Milinski et al. 1995). In contrast to such distraction, foragers may aggregate because they benefit from being in a group or because they use the presence of conspecifics to assess the quality of certain parts of the environment. This aggregation, or conspecific attraction, leads to more extreme patterns of prey depletion, similar to what we found (Beauchamp et al. 1997). It is also conceivable that under certain conditions foragers with different PLT tactics might co-exist. Studies on snails have suggested that foragers with different foraging traits related to the resource acquisition can co-exist as long as there is a trade-off between the ability to utilise the resource and finding the resource (Chase et al. 2001). In our case, it is however hard to imagine how such a trade-off could apply. In any case, co-occurrence of swans with either PLT tactic would not lead to the observed increase in the coefficient of variation, because the depletion pattern would still be heavily affected by swans with a flexible PLT (because they tend to stay longer in the habitat than swans with a fixed PLT).

Alternatively, swans may be constrained in one way or another that prevents them from using the flexible PLT. The swans may for instance not be able to take their past foraging experience into account during foraging, but instead base all their decisions on current intake rates. Although we cannot exclude this possibility, this seems unlikely in the light of experimental evidence for memory effects on foraging behaviour in other bird species (Plowright and Shettleworth 1991, Cuthill et al. 1994). Or, contrary to what was assumed, the instantaneous intake rate may not be a good proxy for the tuber biomass density. Field data indicate that tuber biomass density increases with burial depth (Santamaria 2002, Santamaría and Rodríguez-Gironés 2002). Tuber biomass density in the 0-15 cm burial depth layer is furthermore not correlated with that in the 15-30 cm layer (B.A. Nolet and O. Langevoord, unpublished). This means that the swans have to dig a pit to considerable depth before they obtain reliable information about the local quality. Thus, the intriguing possibility exists that swans superficially behave as foragers with a fixed PLT, although they are in fact using a constrained version of a flexible PLT. The third dimension has been taken successfully into account to explain intake rates and diet choice of waders Charadriiformes feeding on benthic prey. Because prey profitability decreases with burial depth due to an
increase in prey handling times, these birds modify probing depth with prey density (Wanink and Zwarts 1985, Zwarts et al. 1996).

In conclusion, although a flexible PLT is predicted to be the best tactic under exploitative competition, the observations on patch use and prey depletion were more in accord with a model with foragers using a fixed PLT. On the whole, however, the observations were somewhere in between the predictions of a model with a fixed PLT and those of a model with a flexible PLT. This might point at hitherto ignored aspects such as social behaviour and the third spatial dimension which may have a large effect on the spatial pattern in prey depletion by foraging swans.

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