General introduction

An example of spatial variance in the abundance of Fennel pondweed tubers. These samples originate from adjacent subplots.
'In the last quarter of this century, the discipline of ecology has appeared to experience a shift in paradigm. We have become acutely aware that the ecological world is spatially patterned and patchy, that it varies through time in complex and sometimes unpredictable ways. We have embraced the view that the world is heterogeneous and nonequilbirial. We have abandoned the hope of ecological meaning in some idealized, uniform and constant environment' (Sparrow, 1999)

The large amount of time and energy that animals devote to foraging, underlines that foraging is a very important aspect of an animal’s life. MacArthur and Pianka (1966) were among the first to acknowledge that an animal can make choices during foraging, for example about which prey to feed on and how long to feed in a patch, and that something like the best choice exists, leading to foraging in the most economical way. From here, it is only a small step to comprehend that optimal foraging behaviour can evolve by natural selection, assuming that behaviour has a genetic basis and that enhanced foraging is linked to a higher fitness (Stephens & Krebs, 1986). Consequently, foraging ecology can be considered as a subdiscipline of evolutionary ecology (Brown, 2000).

Animals live in a heterogeneous world, as pointed out by Sparrow (1999), thus the act of foraging is played in a spatially heterogeneous setting. Points in space (i.e. locations) might be heterogeneous in for example food abundance (Wiens, 2000), food quality (Moore and Foley, 2005), energetic exploitation costs (Nolet et al., 2001b), food accessibility (Nolet et al., 2006a) or predation risk (Brown et al., 1988). Spatial heterogeneity in any such feature creates an opportunity for animals to make choices that can enhance the efficiency of their foraging activities. For example, heterogeneity in the abundance of food allows a forager to concentrate foraging effort in profitable areas (Valone & Brown, 1989). For this reason, spatial heterogeneity is considered to be, in most cases, beneficial for a forager (Sparrow, 1999). Regardless of the value of spatial heterogeneity for a forager, acknowledgement of heterogeneity is a key to understanding optimal foraging behaviour (see Brown (2000) for an overview).

**Heterogeneity in the abundance of food**

Most, if not all, food distributions are spatially heterogeneous in the abundance of food items. But what exactly is spatial heterogeneity? I follow the classification by Li & Reynolds (1995) and Wiens (2000) and distinguish two basic forms of heterogeneity in the abundance of food items: spatial variance and spatial pattern.

If you sample the abundance of food items at a number of locations you will see that the density (i.e. abundance divided by area, for example the area of the sampling device) varies for different locations. This form of spatial heterogeneity I will refer to as spatial variance: the variation in the abundance of food items at different points in space (Li & Reynolds, 1995; Wiens, 2000). Much spatial variance means that the differences in densities are large.
Figure 1 A-C. Examples of random, clumped and regular spatial configurations of full (grey squares) and empty (open squares) food patches. The distance between the centres of two adjacent patches is 1 m. D-F. Corresponding variograms (see text) for the random, clumped and regular spatial configurations. The horizontal grey line is the level of variance in food density for the whole environment. G-I. Corresponding structure functions (see text) for the random, clumped and regular spatial configurations. Black dots are the probability that a patch is full at a distance $i$, given that the current patch is full. Open dots are the probability that a patch is full at a distance $i$, given that the current patch is empty. The horizontal grey line is the equal probability that a patch is full or empty.
Spatial variance can be described by the frequency distribution of food densities, which can follow a Poisson, a binomial or a negative-binomial distribution (Rodríguez-Gironés & Vásquez, 1997; Green, 1984; 1987). A negative-binomial frequency distribution is commonly observed in natural systems (Pielou, 1977) and means that most locations are poor and only few locations are rich in food.

Different food densities typically do not occur randomly throughout the environment, but spatial pattern in the distribution of densities exists (Rossi et al., 1992). For example, high densities might be observed only in one corner of the area that is surveyed, rather than at random throughout this space. This aspect of a heterogeneous environment I will refer to as spatial pattern: the spatial distribution of densities throughout the environment (Li & Reynolds, 1995; Wiens, 2000). Spatial distributions can be random, clumped or regular (see figure 1 A-C for examples). Only in a random configuration no spatial relationships between locations exist. In a clumped configuration a positive spatial autocorrelation in food abundance exists, which means that high densities are found near other high densities, and low densities are found near other low densities (Legendre, 1993). In a regular configuration a negative spatial autocorrelation in food abundance exists. Many natural spatial patterns are clumped (Rossi et al., 1992; Rietkerk et al., 2004). Spatial pattern implies some repeatability or predictability in the abundance of food.

**Describing spatial pattern**

Spatial pattern can be depicted in a variogram, which is a model that describes the variation in food abundance between pairs of points, as a function of the separation distance of these points (after Rossi et al., 1992). A low value in the variogram means that the differences in food abundance are small for the pairs of points with that particular separation distance. For example, for a clumped configuration of food densities the variogram value is typically low for a small separation distance, and increases with an increasing separation distance up to some maximum that is related to the overall variation in food abundance (Rossi et al., 1992). In figure 1 D-F variograms for random, clumped and regular configurations are presented.

An alternative way to describe spatial pattern, more from the foragers’ perspective, is by structure functions, which are probabilities that a point at distance \(i\) from the current point is in a certain resource state, given the resource state at the current point (Mangel & Adler, 1994). For example, for a clumped configuration of food densities the probability that the food density is high in a nearby patch is high if the food density in the current patch is high and, *vice versa*, low if the food density in the current patch is low. In figure 1 G-I structure functions for random, clumped and regular distributions are presented.
**Discrete and continuous environments**

There are different ways in which suitable foraging habitat can be distributed throughout the environment. In a discrete environment, suitable foraging habitat occurs in clearly delimited units, called patches. Food items are only found in patches and the area in between patches is devoid of prey (cf. for example Charnov, 1976). A field of White clover flowers *Trifolium repens* is an example of a discrete environment for a nectar feeding Bumblebee (Heinrich, 1979). In a continuous environment prey can be found everywhere (Arditi & Dacorogna, 1988; Benhamou, 1992; Bond, 1980). No clear boundaries, except the boundaries of the environment itself, are present that enclose suitable foraging habitat. An example of a more continuous environment is a mudflat for a shorebird searching for invertebrate prey (for example Pienkowski, 1983). A schematic example of a discrete and a continuous environment is presented in figure 2.

![Figure 2](image)

**Figure 2** Example of a discrete (left) and continuous (right) heterogeneous environment. Grey shading indicates habitat where food items potentially can occur. In a discrete environment the area in between patches is devoid of prey. Foraging patches cannot be recognized prior to foraging in a continuous environment.

In part, the distinction between discrete and continuous environments is a matter of scale. Every patch in a discrete environment can be considered as a continuous environment in itself, if viewed at a minute scale. The other way around, a continuous environment can be seen as a discrete patch if viewed at a large spatial scale, for example the landscape scale. Consequently, the way the environment is perceived by the forager, discrete or continuous, also depends on the scale at which the forager approaches the environment.

**Defining patches in discrete and continuous environments**

In a discrete environment it is rather straightforward to recognize foraging patches; they are the clearly delimited spatial units that might contain food. For example, one flower in a field of flowers can be considered as a foraging patch for a nectar feeding bumblebee (Heinrich,
1979). However, what if this forager is able to partition the patch into profitable and non-proitable area (Schmidt & Brown, 1996), in this example if the bumblebee is able to distinguish between different florets in a flower head? Should we consider each floret as a patch? Kotliar & Wiens (1990) emphasized the idea that patchiness is hierarchical. Patches can be found within patches that are found within patches. The patch level relevant for foraging studies is the level at which the forager makes decisions. In this example bumblebees seem to make decisions about flower heads rather than individual florets (Heinrich, 1979), thus flower heads rather than florets should be considered as foraging patches.

But what about defining patches in a more continuous environment? How can we think about spatially delimited units when boundaries are absent? In continuous environments foraging patches cannot be recognized a priori, but are "invented" by the foragers during exploitation (Kacelnik & Bernstein, 1988). Consider for example a Bison *Bos bison* that digs craters in a layer of snow to forage on vegetation (Fortin, 2003). Prior to foraging we cannot point out the patches the Bison will exploit. However, after foraging we can recognize discrete craters dug by the Bison. In accordance with discrete environments a foraging patch is defined as the spatial unit over which a forager makes a decision. Thus, a crater is a patch for a Bison (Fortin, 2003), the area exploited without moving the (front) legs is a patch for an ungulate (also called foraging station, Focardi *et al.*, 1996), and the area probed during one step is a foraging patch for a shorebird (Van Gils, 2004).

**Scale**

The level of heterogeneity in the abundance of food is strongly linked to the scale of observation (Levin, 1992; Wiens, 1989). This can be shown in a small exercise. Imagine an environment that consists of 256 \times 256 cells. Each cell has an equal probability to contain 1 food item or to be empty (random spatial pattern). A portion of such an environment is depicted in figure 3a. Imagine that I sampled the abundance of food items in this environment with a square that has a width of 1, 2, 4, 8, 16 or 32 cells. Irrespective of the width of my sampling square, I observed an average of 0.5 food items per cell. However, the variation in food density that I observed is a decreasing function with an increasing width of my sampling square (Fig. 3b,c).

Foragers also sample the environment at a certain scale, which consequently determines the spatial heterogeneity that they respond to. The smallest scale at which an animal responds to heterogeneity is called the grain. The lower limit of this grain is set by the morphological or perceptual abilities or the behaviour of the forager (Kotliar & Wiens, 1990). Experiments of Kawata and Agawa (1999) showed that freshwater snails did not respond to existing spatial heterogeneity if this was present at a minute scale, which corroborates the existence of a grain. The extent is defined as the largest scale of heterogeneity to which an
Figure 3 A. Environment consisting of $100 \times 100$ cells. Each cell has an equal probability to be full (filled squares) or empty (open squares). Consequently, no spatial pattern exists in this environment. B. Relative frequency distributions of food densities as observed with squares that differ in size (width, in number of cells). Note that the average density observed is 0.5 for all sizes of squares. C. Variation in observed densities if sampled with squares that differ in size (width, in number of cells).
animal responds. Heterogeneity is only relevant to a forager if the scale at which this heterogeneity occurs falls in between the limits of grain and extent (Kotliar & Wiens, 1990).

Given the effect of the scale of observation on the heterogeneity observed, it is important to describe spatial heterogeneity at the same scale as the forager responds to it, which is in most cases at the grain. Unfortunately, in many studies the scale of measurement was determined by the size of the sampling device, rather than by the scale at which the forager responds to heterogeneity.

**Optimal foraging in a heterogeneous world**

*Background theory*

Spatial heterogeneity in the abundance of food provides a forager the opportunity to bias foraging effort towards areas that are, on average, richer in food (Valone & Brown, 1989). Optimal foraging behaviour is the response to achieve this in the most profitable way. Optimality foraging models have three basic components: the decision the forager has to make, the currency that is optimized and the constraints to the possibilities of the forager (Krebs & Davies, 1993; Stephens & Krebs, 1986). In a heterogeneous food distribution, a forager has to decide on 'how long to remain in a patch' (optimal patch use) and on 'how to move between patches' (optimal movement pattern) to enhance the profitability of its foraging activities (Stephens & Krebs, 1986; Green, 1987). Fitness is the ultimate currency to maximize for a forager, but because it is difficult to measure the effect of a foraging decision in terms of fitness, foraging decisions are usually evaluated in terms of energy gain rate, in which it is assumed that an enhanced gain rate is related to a higher fitness (Pyke et al., 1977; Stephens & Krebs, 1986). Factors that limit the performance of a forager are considered to be foraging constraints. Information about the distribution of food is vital to a forager because a forager is dependent on information to make decisions: the better the forager is informed, the better it can adjust its behaviour (Dall et al., 2005; Valone & Brown, 1989).

*Optimal foraging when prey are cryptic*

In many natural situations the position and quality of patches is unknown prior to foraging, for example because prey are cryptic or hidden (buried). Or to put it the other way around: possibly in all natural situations foragers are not completely informed about the position and content of all patches prior to foraging. Incomplete information about the food distribution is a severe complication for a gain rate maximizing forager. In some cases a forager might be able to instantaneously recognize the quality of a patch upon arrival in the patch, for example via olfaction, vision or other sensory cues (Valone & Brown, 1989), but this seems to be the exception rather than the rule. Normally, a forager can only learn the content of a specific patch by sampling it.
The knowledge about the content of a patch that a forager acquires during exploitation is called ‘patch sample information’ and typically includes the number of prey found in the time spent foraging within the patch (Valone, 1989). However, a forager might have access to other sources of information about the content of patches. For example, it might have learned characteristics of the food distribution during earlier visits to the environment. This might include for example the spatial variance and/or the spatial pattern of the food distribution. This form of information that is available prior to foraging is called pre-harvest information. Pre-harvest information can be used to improve the decisions on time in patch and movement between patches, and consequently enhanced gain rate (Valone, 1989; Valone & Brown, 1989). In social environments (i.e. a group of foragers) a forager additionally has access to so-called public information, which is information about the content of patches that is acquired vicariously by monitoring the successful and unsuccessful sampling activities of others (Valone & Giraldeau, 1993; Valone & Templeton, 2002). Social foragers (further) enhance the efficiency of their foraging activities by combining (personal) patch sampling information with public information.

Optimal foraging in a world with cryptic prey, i.e. in which the forager is incompletely informed about the content of patches prior to foraging, received a lot of attention in the literature about foraging behaviour (see Dall et al., 2005 for an overview). Two directions can be recognised in these studies, which are related to different forms of heterogeneity. Studies on patch use focussed on spatial variance and considered the problem ‘how long to remain in a patch’. Studies on movement pattern focussed on spatial pattern and considered the problem ‘how to move between patches’.

1. Patch use in relation to spatial variance under incomplete information

In his Marginal Value Theorem Charnov (1976) described the optimal use of depletable patches that differ in food abundance (spatial variance) for a forager that is omniscient about the quality of patches. A patch should be left as soon as the instantaneous intake rate in the current patch drops to the long-term gain rate that can be achieved in the whole environment. This model was a breakthrough in the field but was also criticized for assuming that food intake is a continuous process, where in reality food items are often discrete. A second criticism involved the assumption that a forager is omniscient about the food distribution, whereas in reality foragers are commonly constrained in the amount of information, as outlined above (Green, 1990; Iwasa et al., 1981; Oaten, 1977). Later theoretical treatments about patch use focussed on the optimal patch use behaviour if prey are discrete and cryptic items, for foragers with different amounts of information on the food distribution and for environments with different frequency distributions of food densities (Poisson, binomial or negative-binomial) (Green, 1984; Olsson & Holmgren, 1998). In general, patch use models have two important assumptions in common: it is assumed
that the environment is discrete (with the notable exception of Arditi & Dacorogna, 1988), and it is assumed that no spatial pattern exists in the distribution of food densities.

2. Movement pattern in relation to spatial pattern under incomplete information
The observation that a forager intensifies its search after it found a food item by modifying its foraging path (a process called area-restricted search), prompted the study of animal movement in environments with cryptic prey (Benhamou, 1992). Models focussed on the efficiency of area-restricted search in environments with different spatial distributions of food densities. An important assumption in these models is that a trade-off exists between the probability to find food and the speed of the forager (Gendron & Staddon, 1983). We can distinguish between one-dimensional models, in which an area-restricted search was modelled as a reduction in speed (Knoppien & Reddingius, 1985; Krakauer & Rodríguez-Girones, 1995) and two-dimensional models, in which an area-restricted search was modelled as a reduction in speed and an increase in the sinuosity of the foraging path (Benhamou, 1992). In clumped food configurations, an area-restricted search after a food item capture enhances the energy gain rate since more time is spent in area that is relatively rich in food. In the one-dimensional models this is solely the effect of the tendency to move slower in richer area. In the two-dimensional models this is in addition the result of encountering relatively rich area at a higher frequency as it is on offer. Studies on animal movement in relation to spatial pattern have in common that it is assumed that the environment is continuous.

Aims and outline of this thesis
The central research theme in this thesis is how foragers should use patches (time in patch) and move in between patches (movement length), in order to maximize their energy gain rate, in an environment that is heterogeneous in the abundance of cryptic food items. There is a focus on effects of spatial pattern on time spent in patches and movement between patches. Inspired by the pioneering studies of Van Eerden et al. (1997) we chose the Bewick’s swan foraging on belowground Fennel pondweed tubers as the main study system. Bewick’s swans search for the patchy distributed tubers upon touch, which makes this system very suitable for our research (see Box I). The fact that swans are gregarious receives a considerable amount of attention throughout this thesis. Some ideas are investigated in a laboratory experimental setup, but for practical reasons we used Mallard rather than Bewick’s swans (see Box II).

I. Theory and field observations
The first paper of this thesis (chapter 2) is a theoretical treatment about optimal movement in relation to spatial pattern in the distribution of cryptic food. The aim of this exercise was to determine the optimal movement rule (i.e. the rule that maximizes the
energy gain rate) in environments with different spatial patterns (random, clumped or regular configuration), for a forager that knows the specific spatial pattern in the distribution of food. Furthermore I wanted to know in which specific environments such prior knowledge about spatial pattern is valuable to a forager. In relation to this theoretical model I tested in the field whether Bewick’s swans foraging on Fennel pondweed tubers use pre-harvest information about spatial pattern in the distribution of tuber biomass densities, and whether they use this information in the most economical way (chapter 3). This required not only a meticulous description of the movement pattern of swans in an environment with manipulated food densities but also a detailed picture of the natural spatial pattern in the distribution of tuber biomass densities.

Bewick’s swans are gregarious and forage in flocks. To further enhance the understanding of movement patterns in the field I studied the effects of social interactions on the movement pattern of swans in relation to the social status of swans in chapter 4. The fact that swans are social foragers might also affect their use of patches, since a swan foraging in a flock competes for food with its conspecifics. To gain insight in the patch leaving behaviour of flock-feeding swans I compared observed patch leaving behaviour and tuber exploitation patterns with predictions for foragers with a fixed critical threshold to leave patches (expected for solitary foragers) and for foragers that readjust their critical threshold during depletion of the habitat (expected under exploitative competition) (chapter 5).

Given the significance of spatial heterogeneity for the foraging behaviour of swans it is interesting to understand where this heterogeneity comes from and how it is maintained. In chapter 6 I describe how different biological processes, including the foraging activities of swans, impinge on spatial variance and spatial pattern in the distribution of pondweed tuber densities, to elucidate why variance and pattern remain in the system.

II. Laboratory experiments

An important aspect of foraging in a heterogeneous environment is how an animal experiences its environment. In an experiment with tactile feeding Mallard, I determined whether ducks were able to respond to existing heterogeneity, also when this occurred at a very small scale (chapter 7). The aim was to illustrate that something like a foraging scale (grain) exists below which ducks cannot respond to existing heterogeneity, and to determine how this affects the duck’s food intake rate.

In chapters 2 and 3 I investigated how spatial pattern affects movement patterns of swans. Apart from an effect on movement pattern, spatial pattern could also affect the assessment of patches (i.e. whether the next patch is expected to be good or bad). In a laboratory experiment I investigate how spatial pattern in the distribution of food densities affected patch assessment in foraging Mallard, by determining patch use in environments with different spatial patterns (random, clumped and regular configuration) (chapter 8).
BOX 1. Study system I: Bewick’s swans foraging on Fennel pondweed

The Bewick’s swan *Cygnus columbianus bewickii* is a long-distant migrant that has its breeding grounds in subarctic Russia and winters in Western Europe, mainly in Great Brittan and The Netherlands (Western Palearctic flyway population). Swans cannot complete their impressive migratory journey in a single 3500 km flight, but make several stops *en route* to refuel (Beekman *et al*., 2002). Autumn migration is much faster than spring migration, which is related to different environmental conditions the swans face during the different seasons (Beekman *et al*., 2002). At stopover sites swans almost solely forage on belowground tubers of Fennel pondweed *Potamogeton pectinatus* (Beekman *et al*., 1991; Van Eerden *et al*. 1997). At the wintering grounds few swans retain aquatic feeding on waterplants, but the majority of swans switches to terrestrial feeding on agricultural harvest leftovers (beets) and grass (Dirksen *et al*., 1991).

Lauwersmeer (53°N 06°E, The Netherlands) is a former estuary that developed into a freshwater lake after its embankment in 1969. Fennel pondweed rapidly spread after its colonization in 1972, and has dominated the macrophyte community up to now. Swans started to use the area for a stopover already in 1973. Lauwersmeer is the last stopover site in autumn (October), before wintering grounds are reached. When the pondweed tuber stock gets depleted swans switch to terrestrial beet-feeding or directly leave for their wintering grounds (Nolet *et al*., 2002).

Fennel pondweed is a pseudo-annual freshwater macrophyte that survives the winter by asexually produced tubers. Tubers can differ up to eightfold in size, in which larger tubers are buried deeper in the sediment (Santamaría & Rodríguez-Gironés, 2002). On average, the largest number of tubers is found at an intermediate burial depth of 7.5 cm, whereas the largest tuber biomass is found at maximum burial depth of 27.5 cm (Santamaría & Rodríguez-Gironés, 2002). Tuber biomass densities in the upper layer of the sediment are not related to biomass densities deeper in the sediment (B.A. Nolet, O. Langevoord, unpublished). Deeply buried tubers can be out of reach of swans, especially in less shallow parts of the lake, which creates spatial refuges for tubers against swan predation (Santamaría & Rodríguez-Gironés, 2002; Nolet *et al*., 2006a).

Swans trample their feet to loosen the sediment and subsequently retrieve tubers by sieving sediment with their heads submerged (see figure B1). Trampling creates a crater, which is depleted in a series of foraging bouts (Brouwer & Tinbergen, 1939). At the time of exploitation in autumn, aboveground biomass and belowground roots have died off. Consequently tubers can be considered to be cryptic to the swans (Van Eerden *et al*., 1997). Spatial variation in tuber exploitation by swans is related to differences in net intake rates, in which gross gain rates are lower and energy expenditure is higher at clayish sites (Nolet *et al*., 2001b). In autumn, swans seem to maximize their daily energy intake rather than satisfying their daily requirements (Nolet *et al*., 2002; Nolet & Klaassen, 2005). Daily energy intake of pondweed feeding swans is limited by time rather than the capacity to processes food (Nolet & Klaassen, 2005).
Bewick's swans are strongly gregarious and forage in groups. A strong social hierarchy is observed in which families with young are dominant over paired swans without young, whereas singletons are lowest in rank (Van Eerden et al., 1997; Badzinski, 2003). Swans defend their crater to other swans, except to a partner or young. Families forage in richer parts of the pondweed bed, and leave the bed earlier (i.e. give up at a higher density) than paired swans and singletons (Van Eerden et al., 1997).

A pondweed bed can be considered as a continuous environment for a foraging swan. A crater presumably represents a foraging patch, and measures about 1m$^2$ (Van Eerden et al., 1997). Pondweed tuber abundance varies considerably throughout the pondweed bed. In part this is explained by sediment characteristics, in which tuber densities tend to be higher at more clayish sites. However, also within sediment classes a strong spatial variance in tuber biomass density is observed (Nolet et al., 2001b). Differences in the biomass densities are primarily caused by differences in the number of tubers and not by differences in the size of tubers (Nolet & Klaassen, 2005). Tuber biomass densities are not randomly distributed throughout a pondweed bed but pondweed seem to occur in clumps with a diameter of roughly 10 m (clumped spatial pattern) (Nolet & Mooij, 2002). Large scale movement pattern and search behaviour of swans seems to be causally linked to this large scale spatial pattern, where swans alternate between an extensive (high speed, directed) and an intensive (low speed, sinuous) search mode (Nolet & Mooij, 2002).

For several reasons, the Bewick's swan – Fennel pondweed system provides an excellent opportunity to study the optimal foraging behaviour of swans in relation to the small scale spatial heterogeneity in tuber abundance. Firstly, it is a well-studied system, so for example, the swans’ functional response, energy expenditures of different behaviours and foraging currencies are known (see Van Eerden et al., 1997; Nolet et al., 2001b).
2001b; 2002; Beekman et al. 2002; Nolet & Klaassen, 2005). Secondly, in autumn tuber abundances do not change considerably, except of course due to the foraging activities of swans. Consequently, food abundance can be accurately mapped just before and just after the foraging by swans, in which changes in abundance can be fully addressed to swan foraging. Thirdly, the exploitation period is a relatively short period in the year (it lasts only a few weeks), whereas it has a large impact on the ecosystem (Jonzen et al., 2002; Nolet 2004). Finally, tuber densities appear to be non-randomly distributed throughout a pondweed bed, and swans appear to respond to this spatial patterning, at least at a larger spatial scale (Nolet & Mooij, 2002).

A disadvantage of this study system for foraging studies is that exact food item captures cannot be observed, since the swan’s head is submerged in turbid water during food item captures, in contrast to for example waders (Van Gils, 2003) and cranes (Alonso et al., 1995). Nevertheless, consumption rates can be derived from food densities estimates and the swan’s functional response, thus an estimate of the amount of food collected can be assessed per individual foraging bout. Another disadvantage is the fact that the sampling of tuber abundance is extremely laborious, which means that it is impossible to obtain a detailed picture about the tuber abundance from a very large area.

BOX 2. Study system II: Mallard as a model for Bewick’s swans

Laboratory experiments on aquatic feeding Bewick’s swans can be extremely laborious, given their large size and the relatively large amounts of sediment and food items required. In order to keep experiments feasible, we choose to investigate some ideas in an experimental setting using the much smaller Mallard *Anas platyrhynchos*. In the field, Mallard are frequently observed to forage on small cryptic prey buried in the sediment. We used commercially available husked millet or wheat seeds as prey items. Mallard retrieve seeds by sieving sediment through their bill (Kooloos et al., 1989).

In general, the feeding behaviour of Mallard and Bewick’s swans is very similar, thus Mallard seems to be an appropriate model for the Bewick’s swan. However, there are two important differences between feeding Mallard and feeding Bewick’s swans that should be taken into account while extrapolating results obtained for Mallard to the ecology of swans. Firstly, Mallard can filter sediment without submerging their head, in contrast to aquatic feeding swans that have to up-end to reach the sediment. Consequently, a foraging bout of a swan closely resembles the dive of a duck (De Leeuw 1996), rather than the filtering foraging mode of the Mallard. Secondly, Mallard to not create discrete craters during foraging, in contrast to swans, but exploit the environment in fairly continuous lines. Consequently, it might be straightforward to recognize patches after foraging by swans (each crater is a patch) but complicated to recognize patches after foraging by Mallard (the area covered during one step might be considered as a patch).