Foraging in a spatially patterned world
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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2006

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

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Download date: 06-12-2018
General discussion:

How spatial pattern in the distribution of Fennel pondweed tubers shapes migratory patterns of Bewick’s swans

A part of the flock of Bewick’s swans takes a late-afternoon rest in the Babbelaar, Lauwersmeer. The birds in the background remain foraging.
Introduction
The idea that an environment or a habitat is homogeneous is an oversimplified view of reality (Sparrow 1999). Just try to think of an example of an entirely homogeneous habitat (I bet you can’t find a single one). Spatial heterogeneity, i.e. discontinuity in space, is the norm. Nevertheless, in many studies spatial homogeneity was assumed for convenience and simplicity, and heterogeneity was considered as a necessary evil or an unwelcome complication (Pickett & Cadenasso 1995; Wiens 2000). Nowadays, it is becoming increasingly clear that the functioning of an ecosystem can only be understood by explicitly considering heterogeneity, and that effects of heterogeneity on individuals, populations and communities is a study in itself (Stewart et al. 2000). An illuminating example is the coexistence of (plant) species that differ in their competitive abilities. Long-lasting coexistence can only be explained by acknowledging spatial heterogeneity in the abundance of the dominant species, since this creates refuges for less competitive species that would be outcompeted in a homogeneous setting (Stoll & Prati 2001; Tilman 1994).

The world of the migratory Bewick’s swan Cygnus columbianus bewickii is likewise heterogeneous. We can view this world at different spatial scales, ranging from foraging patches to the entire migratory flyway, in which discontinuities in space are observed at each spatial level. This world is hierarchical, i.e. each spatial entity consists of several spatial entities that are in turn composed of several spatial entities at a smaller scale, etc. (see Kotliar & Wiens 1990; Fauchald 1999; figure 1). I define a foraging patch as the smallest spatial unit over which a forager makes a decision (see also chapter 1). For a Bewick’s swan feeding on Fennel pondweed Potamogeton pectinatus tubers a foraging patch is equal to the crater that a swan digs to retrieve the deeply buried tubers. Patches are not randomly distributed throughout the area, but patches with relatively similar food densities are found together in so-called clumps that measure about 10 x 10 m (Nolet & Mooij 2002). Many such clumps are found within a pondweed bed, which is delimited by shorelines and gullies. Several pondweed beds are in turn found within a lake or bay. Finally, a number of lakes, bays, and the breeding- and winter grounds make up the flyway of the Bewick’s swan.

Every level in this hierarchy involves specific optimality decisions (Stephens & Krebs 1986; Kotliar & Wiens 1990; Fauchald 1999). At the scale of patches a swan has to decide on the time it spends in a patch, whereas at the scale of the flyway a swan has to decide on whether it should use a lake for a migratory stopover or carry on to the next (see Beekman et al. 2002). Figure 1 shows to which spatial scales the different chapters in this thesis are related. At a glance it becomes clear that my work focussed on processes acting at the smallest spatial scales. In this chapter I will show that insight in the behaviour of animals at a small spatial resolution is key to understanding processes that act at much larger spatial scales (see e.g. Fryxell et al. 2005). In particular, I link the swans’ foraging responses to small scale spatial heterogeneity in food abundance to their migration strategy and reproductive success. Furthermore, I show that in some cases it is important to
acknowledge small scale heterogeneity in the abundance of food for carrying capacity calculations.

The impressive journeys of the Bewick’s swan
The migratory Bewick’s swan has an extremely short time window for successful reproduction. At their sub-arctic breeding grounds the frost-free period lasts about 120 days, whereas swans need about 110 days to complete their breeding cycle (from territory establishment to fledging of young) (Beekman et al. 2002). Consequently, it is important for a swan to arrive on time at the breeding site to preserve a prospect for successful reproduction. Arriving too early might be disadvantageous, since the frozen state of the landscape denies access to food. Nevertheless, because swans compete for good territories (Beekman et al. 2002), it is predicted that they arrive at a date that precedes the optimum date in absence of competition (Kokko, 1999).

Figure 1 Hierarchical patchiness in the world of the Bewick’s swan; scaling up from foraging patches to the swans’ flyway. For every spatial scale (i.e. level of patchiness) relevant optimality decisions that the swans have to make are listed. Encircled numbers refer to different chapters of this thesis.
Figure 2 Fitness in relation to the date of arrival at the breeding ground, for birds that differ in arrival condition. 1: birds arrive lean (without extra reserves), 2. birds arrive with a moderate amount of reserves, 3. birds arrive with the maximum amount of reserves. Black dots indicate the earliest possible arrival date for a bird: Birds that travel light can arrive earlier than birds that arrive with larger amounts of energy stores. The upper panel represents a scenario in which there is no competition for territories, whereas the lower panel represents a scenario in which birds that arrive early occupy the best territories. Based on Prop et al. (2003).

Three to four thousand km separate breeding and wintering grounds for the Western Palearctic flyway population, whereas the maximum flight distance that swans can cover without refuelling is 2,000 km (Beekman et al. 2002). Consequently, with or without wind assistance, swans cannot complete their migratory journey in a single flight, but must make several stopovers en route, to replenish fuel stores, which they do by aquatic-feeding on energy-rich tubers of Fennel pondweed (Beekman et al. 2002). A swan arriving late at a stopover site is confronted with a depleted food stock and/or sprouting tubers (in spring only), which is linked to a reduced refuelling rate (Nolet & Drent 1998). On the other hand, the time of arrival at a stopover site is limited in spring by ice break-up along the migratory route (Beekman et al. 2002). Given the strong competition for food we might expect that the swans that migrate closely behind the sequence of ice break-up along the migratory route are the most successful breeders. However, successful reproduction for such large
birds at northern latitudes requires bringing energy reserves along that can be used to prepare eggs and incubate them (Drent & Daan 1980; Klaassen et al. 2001). Since there is a trade-off between arrival date and energy stores upon arrival it is expected that individuals that arrive slightly later, though with more energy reserves, achieve the highest fitness (Prop et al. 2003, figure 2). Competition for good breeding territories might alter this picture and favour birds that arrive slightly earlier, though with fewer energy stores (figure 2).

Irrespective of whether swans minimize the time of migration or maximize the amount of energy they bring to the breeding grounds, it is expected that swans maximize their energy gain rate at stopover sites in spring (Hedenström & Alerstam 1998). In autumn swans pass-by (skip) a stop-over site that is extensively used in spring (White Sea) which is explained by this site being of a much lower quality than the preceding site (Pechora delta, their autumn starting point, see Beekman et al. 2002). The phenomenon that a possible staging site is skipped is only expected for time-constrained migrants, thus we can expect that swans also in autumn maximize their energy gain rate at stopover sites (Beekman et al. 2002). The maximum daily metabolizable energy intake of a swan feeding on pondweed tubers appears to be limited by foraging time rather than their capacity to process food (Nolet & Klaassen 2005). Nolet and Klaassen (2005) suggested that this is related to the fact that feeding by swans can be considered as a form of diving, since swans submerge their head and half of their body during feeding. Diving animals do not fully maintain body temperature during feeding, and body temperature cannot be restored during the short periods of surfacing interspersing feeding events. Consequently diving imposes a considerable time cost since diving animals need long resting and preening sessions to recuperate body temperatures (Nolet & Klaassen 2005). In the next paragraph I will discuss how a forager can maximize its energy gain rate in an environment that is heterogeneous in the abundance of food.

**Exploitation of heterogeneously distributed food**

Food distributions, such as the distribution of Fennel pondweed tuber densities, are typically heterogeneous (Sparrow 1999; Wiens 2000; see also chapters 1, 3 & 6). Basically, there are two ways in which a forager can enhance its energy gain rate in relation to spatial heterogeneity in the food distribution, (1) by regulating exploitation time within a patch and (2) by regulating movement in between patches (see also chapter 1).

**Regulating time within patches**

Spatial variance in the abundance of food allows a forager to bias its searching effort towards rich patches and away from poor patches (Stephens 1989). To devote time to patches in the most profitable way, a forager has to decide on when to leave a patch. The optimal solution for a solitary forager that is omniscient or prescient (see Valone & Brown 1989) about the quality of patches is to leave a patch as soon as the intake rate in the patch
drops to the maximal long-term intake rate achievable in the particular habitat (Charnov 1976). Intake rate can be translated to prey density, thus omniscient and prescient foragers are expected to leave all patches at the same specific prey density termed “Giving Up Density” or GUD for short (Charnov 1976; Valone & Brown 1989). No time is spend in patches with an initial prey density (IPD) < GUD.

However, most foragers, such as Bewick’s swans, are not omniscient or prescient about patch content because food items are cryptic. Such foragers must first assess the quality of a patch before they can benefit from a more efficient allocation of effort (Olsson & Brown 2006). In order to assess the quality of a patch a solitary forager has two sources of information about the content of the patch: patch sample information, i.e. the number food items found and the time required to find them, and pre-harvest (or prior) information, i.e. characteristics of the food distribution throughout the environment learned during earlier visits (Valone 1989; Dall et al. 2005). The frequency distribution of food densities is the pre-harvest information usually considered in patch assessment models. Bayesian statistics provide a framework how the different sources of information can be combined to assess the content of patches (Iwasa et al. 1981). As pointed out elsewhere (Green 1980, 1988; McNamara 1982; Olsson & Holmgren 1998; Olsson & Brown 2006) the optimal solution for a Bayesian forager is to leave the patch as soon as the estimate of the potential intake rate in the patch drops to a constant critical intake rate. This leads to an interesting patch use pattern in which GUDs are not constant for different IPDs, but a humped relationship between GUD and IPD is predicted (Olsson & Holmgren 2000; Olsson & Brown 2006). In practice this relationship will be linearly increasing which is caused by a skew in the patch quality distribution (see Olsson & Holmgren 2000 for details).

In chapter 8 we point out that the frequency distribution of food densities is not the only form of pre-harvest information that is available to a forager. Different food densities are usually not randomly distributed throughout the environment, but a clear spatial pattern exists (Wiens 2000; see also chapter 1). This spatial pattern is also a form of pre-harvest information because the position of a patch in relation to previously visited patches provides an expectation about the food density in that patch, for a forager that knows the spatial pattern of the food distribution. For example, the probability that a Bewick’s swan finds a high density patch near the current patch is much higher if the density in the current patch is high, than if the density in the current patch is low (figure 3). Whether Bewick’s swans use pre-harvest information about the spatial pattern to assess the quality of a patch could not be studied in the field because the laborious character of the tuber sampling procedure prevents a detailed description of pondweed densities in a large area. To get around this, we investigated this concept in a laboratory experiment (chapter 8) in which we determined the time Mallard Anas platyrhynchos spent searching for buried wheat seeds in full and empty patches, in environments with different spatial configurations of full and empty patches. Mallard appeared to be sensitive to spatial pattern and used this (pre-
harvest) information to enhance their assessment of patches. Such a response to pattern leads to a higher gain rate. Given the similarities between Mallard and Bewick’s swans and their food we have all reason to believe that swans as well take advantage of pre-harvest information about spatial pattern to assess the quality of patches in the field.

Bewick’s swans spend more time in rich than in poor patches (chapter 3), and thus regulate the time in patches in the field. This can also be inferred from tuber depletion patterns. Figure 4 shows the relationship between tuber densities before (initial: IPD) and after (final: GUD) swan grazing. A swan that spends an equal amount of time in every patch removes a fixed proportion of biomass in every patch (assuming a linear functional response, which is justifiable for Bewick’s swans, see Nolet et al. 2002). However, in the field swans consume a higher proportion from rich than from poor patches, as indicated by the intercept of the regression between IPD and GUD being significantly greater than 0 (figure 4). In other words, also from the depletion pattern we can see that swans regulate their time in patches.

Figure 3 The frequency in which a swan expects to encounter different food densities in patches at different distances from the current patch. Intensity of shading indicates the density class (classes 1–4, lowest density class in white, see figure 1 chapter 3 for details). In the upper track the density in the current patch is low (class 1), whereas in the lower track the density in the current patch is high (class 4). Note that a swan that is currently in a poor patch expects to find poor patches nearby, whereas a swan that is currently in a rich patch expects to find rich patches nearby.
Figure 4 Illustration of the exploitation of Fennel pondweed tuber biomass densities by Bewick’s swans. Panel C and panel A show the relative frequency distributions of tuber biomass densities before swan exploitation (October, panel C) and after the foraging of swans (November, panel A). In panel B the relationship between the tuber biomass densities in October against the tuber biomass densities in November is plotted. The solid line represents the linear regression ($y=0.24x + 9.1351$), the dotted line represents the relationship $y=x$. The estimated intercept of this regression equals 9.1 (stdev 2.0) which is significantly larger than 0 ($t_{98}=4.5$, $p<0.001$). Data were collected in autumn 2003 in a 10 x 10 m plot where biomass densities were determined per 1 m$^2$ (see chapter 3).

Interestingly, the slope of the relationship between IPD and GUD is significantly larger than 0 (figure 4), i.e. GUD is an increasing function of IPD. Such positive relationship between IPD and GUD is predicted for Bayesian foragers that leave patches according to a potential assessment rule (Olsson & Holmgren 2000). An alternative explanation for a positive relationship between IPD and GUD is that the forager exploits patches down to a fixed threshold, where a certain fraction of the food in patches is not accessible (i.e. out of
reach, see Nolet et al. 2006). The slope of the regression between IPD and GUD equals the proportion of food that is inaccessible. In the example depicted in figure 4 the slope equals 0.24, thus 24% of the food was out of reach of the swans. The (fixed) GUD practiced by the swans is equal to the intercept of the regression between IPD and GUD, in the example in figure 4 this equals 9.1 g/m². Pondweed tubers that occur deeper than 86 cm from the water surface are out of reach for foraging Bewick’s swans (Nolet et al. 2006). Maximum tuber burial depth is 30 cm, thus whether swans can reach tubers depends on the water level (Nolet et al. 2006). Water depth for our study plot was about 60 cm. Nolet et al. (2006) estimated that in this case exactly 24% of tuber biomass is out of reach for the swans!

Although it remains to be established why swans exploit patches down to the threshold levels we observed, we can conclude that swans regulate their time in patches and consequently profit from existing small-scale spatial variance in the abundance of tuber biomass densities.

Regulating movement between patches

The second way in which an animal can enhance its gain rate in relation to spatial heterogeneity is by regulating the movement between patches. A forager can regulate movement by adjusting the (turning) angle between subsequent movements (i.e. sinuosity of the path) and/or by adjusting the length of movements. Gain rate is enhanced for a forager that moves strategically through the environment as it encounters high densities more frequently and low densities less frequently than they are on offer. This effect was observed both in two-dimensional models in which movement is regulated by changes in turning angles (Benhamou 1992; Fortin 2002), and in one-dimensional models in which movement is regulated by changes in the length of movements (chapter 2). Benhamou (1992) determined the optimal level of sinuosity in relation to differently clumped food distributions. In chapter 2 we determined the optimal lengths of inter-patch movements for different spatial distributions of full and empty food patches (clumped, regular, and a random configuration).

Viewed at the scale at which swans sample the environment (see also chapter 7), a positive spatial autocorrelation in pondweed tuber biomass density was observed (i.e. the distribution of food densities is clumped, chapter 3). We parameterized the one-dimensional movement model introduced in chapter 2 for the swan-pondweed system to predict inter-patch movement lengths for the specific spatial pattern observed in a pondweed bed. A swan that always moves to the patch where it expects the highest gain rate was predicted to move a longer distance from a starting point in a poor patch and a shorter distance from a starting point in a rich patch (defined by tuber biomass density) (chapter 3). To test this hypothesis we conducted an experiment in the field: during different stages in the growing season we removed all aboveground biomass in large
subplots to create plots with different tuber biomass densities. In autumn we subsequently accurately recorded the movement paths of swans foraging in these subplots by taking a triangular fix of the position of the swan every time it submerged its head, by simultaneously measuring the angle to the swan from two hides, using two total station range finders. In accordance with our theoretical predictions it was observed that the inter-patch distance was large for a movement from a patch that had been poor, and small for a movement from a patch that had been rich in food (chapter 3). At this spatial scale, swans only related the length of inter-patch movements to the density of food, and not the angle of these movements, so we can conclude that the fact that the swans perceive a much richer environment than is on offer can be ascribed to regulating movement lengths. Such non-random movement was calculated to enhance the gain rate by 1.4 times (chapter 3). These observations accord well with the large-scale movements described by Nolet & Mooij (2002). At a larger spatial scale, say the scale of the whole pondweed bed, the swans seem to alternate between an intensive (low-speed, sinuous) and extensive (high-speed, directed) search mode. This appears to be an optimal way to locate large (10 x 10 m) food clumps (Nolet & Mooij 2002). Our results elucidate how movement is fine-tuned to the small scale heterogeneity that exists within such food clumps (chapter 3). Taking these two studies together, the foraging behaviour of the swans can be viewed as an adaptive response to this hierarchical patchiness in food abundance (Kotliar & Wiens 1990; chapter 3).

A number of other studies, listed in table 1, also report that foragers respond to spatial pattern in an adaptive way. In some studies the forager regulates the sinuosity of the path whereas in other studies the forager only regulates the length of inter-patch movements. All studies on natural spatial patterns that we are aware of involved clumped configurations of food, which is not surprising since examples of natural non-clumped spatial configurations are rare. However, Lovworn and Gillingham (1996) describe the distribution of densities of belowground winter buds of the submerged plant *Vallisneria americana* as being random, i.e. no spatial correlations in winter bud densities were found. Consequently, a Canvasback *Aythya valisineria* that feeds on these buds has the same expectation of food density regardless of distance moved (Lovworn and Gillingham 1996), thus in this case the length of a movement is not expected to be related to the food density in the patch this movement started. Regular configurations of organisms seems to be the result of competition between conspecifics. Kenkel (1988) for example describes that the distribution of living Jack pines *Pinus banksiana* is regular, which was explained by a strong competition for soil resources and light. Regular patterns were also observed in coastal macrobentic communities in soft-bottom habitats (Thrush 1991). However, all foraging studies devoted to shorebirds preying on benthos that I am aware of concerned clumped distributions of food (e.g. Van Gils *et al.* 2006). Adaptive foraging responses in experimentally induced non-clumped spatial patterns indicate that a response to pattern is not restricted to clumped configurations, which strongly argues for studies on natural spatial patterns that are not clumped.
Table 1 Examples of studies where foragers respond to natural or experimentally induced spatial pattern in the distribution of food by regulating the sinuosity (s) of their path or the length of inter-patch movements.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spatial pattern</th>
<th>Response</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thrushes Turdus sp.</td>
<td>natural: clumped</td>
<td>sinuosity of path (s) is increased after prey encounter</td>
<td>Smith 1974</td>
</tr>
<tr>
<td></td>
<td>experimental:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>- clumped</td>
<td>always increase s after prey encounter</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- random</td>
<td>sometimes increase s after prey encounter</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- regular</td>
<td>never increase s after prey encounter</td>
<td></td>
</tr>
<tr>
<td>Bumblebee Bombus terricola</td>
<td>natural: clumped</td>
<td>length of movements are shorter and sinuosity of path is higher in rich than in poor area</td>
<td>Heinrich 1979</td>
</tr>
<tr>
<td>Starling Sturnus vulgaris</td>
<td>natural: clumped</td>
<td>birds tend to land close to a previous visited patch when foraging success had been high in that patch, and further away when foraging success had been low</td>
<td>Tinbergen 1981</td>
</tr>
<tr>
<td>Grey plovers Pluvialis squatarola</td>
<td>natural: clumped</td>
<td>birds move less far after taking a large prey than after taking a small or no prey</td>
<td>Pienkowski 1983</td>
</tr>
<tr>
<td>Bison Bos bison</td>
<td>natural: clumped</td>
<td>non-random movement results in successfully avoiding poor feeding area</td>
<td>Fortin 2003</td>
</tr>
<tr>
<td>Plaice Pleuronectes platessa</td>
<td>experimental:</td>
<td>intensive search near prey</td>
<td>Hill et al. 2002</td>
</tr>
<tr>
<td></td>
<td>- clumped</td>
<td>always extensive search</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- regular</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bewick’s swan Cygnus columbianus bewickii</td>
<td>natural: clumped</td>
<td>inter-patch distance is long from poor and short from rich patch</td>
<td>chapter 3</td>
</tr>
</tbody>
</table>

Bewick’s swans experience a richer environment than the environment actually on offer due to the strategic non-random way they move through the environment (chapter 3). In other words, there is a mismatch between the average density swans experience and the average density we sample in the field. This is an important result for the interpretation of critical threshold densities observed in the field. The average food density we observe after the exploitation episode is lower than the critical threshold density practiced by the forager, since this forager experienced a richer environment than the environment on offer. Consequently, a response to spatial pattern might explain discrepancies in observed and expected threshold densities. For example, Nolet et al. (2002) reported that Bewick’s swans left a pondweed bed at slightly lower gain rates that swans could achieve at nearby agricultural fields. An alternative explanation for the delayed switch would be that the swans experienced a slightly richer pondweed bed due to their fine-tuned response to pattern, and that swans thus left the pondweed bed exactly at the gain rate that was achieved at the
alternative site, as predicted from an optimal foraging perspective. On the other hand we know that swans markedly reduce the degree of spatial pattern in the distribution of pondweed densities (chapter 6), which would preclude any opportunity to respond to pattern at the end of an exploitation episode.

Costs and benefits of social foraging

The ideas about regulating time in a patch and movement between patches listed above are applicable to an animal foraging alone. However, just as with the assumption that the world is homogeneous, this is a severe simplification of reality. Presumably without exception, animals do not forage solitarily but rather socially, i.e. social foraging seems be the rule rather than the exception. For example, the studies listed in table 1 all deal with socially feeding species. Here I mean with 'social foraging' that energetic gains and losses of the forager are influenced by other foragers (definition cf. Giraldeau & Caraco 2000). There are two important differences between a solitary and socially feeding forager.

Firstly, by watching the behaviours of others, a social forager acquires information about novel prey types, novel behaviours in prey acquisition, location of (high quality) patches, and the quality of patches (Giraldeau et al. 2002). The latter has been termed 'public information' and is defined as sampling information acquired vicariously by monitoring the sampling behaviour of others (Valone and Templeton 2002). By combining the pre-harvest and personal patch sample information with public information, an individual can estimate patch quality faster and more precisely, which results in more efficient resource exploitation (Clark & Mangel 1986; Valone 1989; Valone and Templeton 2002; Sernland et al. 2003).

Bewick’s swans are strongly gregarious and most probably use public information to assess and to keep track of changes in food density. The time a swan spends at a patch, or equivalently the number of foraging bouts (see chapter 3) is a good indication for the quality of a patch. A swan that newly arrives at a pondweed bed can quickly assess the average density of the bed by watching the feeding behaviour of other individuals. However, a swan cannot observe successful and unsuccessful sampling activities by other individuals during feeding, since it then has its head submerged. Since swans have their heads submerged for about half of the time (see chapter 3), access to public information could be constrained by their mode of feeding. Acquisition of public information comes at a cost, as a missed foraging opportunity, if a swan acquires public information by suspending feeding, as pointed out by Giraldeau et al. (2002).

It was beyond the scope of this thesis to establish the use and significance of public information for foraging Bewick’s swans. Nevertheless, a study on the role of public information in the estimation of characteristics of the food distribution (quality and spatial configuration) would be very valuable for the understanding of pondweed exploitation. I would not be surprised if it turns out that access to public information rather than the predation risk is the "main reason" for the flocking behaviour of swans.
Another important difference between a solitarily and a socially feeding forager is that optimal decisions of a social forager depend on the decision or behaviour of other foragers (Giraldeau & Caraco 2000). What is optimal for a solitary forager might be sub-optimal for a social forager. This certainly holds for swans feeding on pondweed. For a swan feeding solitarily, the average food density in the environment is more or less stable (as long as patches are not revisited and tubers do not yet sprout), whereas for a socially feeding swan the food density in the environment progressively decreases over time due to exploitation by conspecifics. In a flock, swans compete for food either directly by fighting over rich patches (interference competition) or indirectly by exploiting patches (exploitative competition). Direct competition might induce a skew in intake rates, since the more dominant swans will occupy the best patches. The dominance rank of a Bewick’s swan is strongly related to its social status, in which singletons are the lowest and families the highest in rank (Van Eerden et al. 1997; Badzinski 2003; chapter 4). Field observations confirm that the most dominant birds (families) occupy the best patches (Van Eerden et al. 1997). Given these differences between foraging alone and in a group we might expect that the optimal time in a patch is also different for solitary and social foragers. We modelled the optimal decision when to leave a patch for swans that keep track of these changes in food abundance (chapter 5). The optimal behaviour was to leave a patch at a fixed threshold for a swan feeding solitarily, and at a flexible threshold for a swan foraging in a flock (chapter 5). In a changing environment, information about food density that is collected during foraging becomes rapidly outdated, so we might expect that foragers continuously update the estimate about the quality of the environment with recent (foraging) information, and that older (outdated) information is disregarded (linear operating model; Bernstein et al. 1988; see also Rodríguez-Gironès & Vásquez 1997). In the simulations we determined the optimal length of the interval between collecting and discarding information (memory trace, a longer interval means that the estimate of the quality of the environment is based on a larger number of patches). Interestingly, a short memory trace, corresponding to only one patch, appeared to be optimal (see chapter 5). Very different food exploitation patterns were predicted for a fixed in comparison to a flexible exploitation rule. Surprisingly, the exploitation pattern observed in the field matched best with the predictions for a fixed threshold. A possible explanation, apart from that swans are not under exploitative competition, is that other factors are also important, for example the depth distribution of pondweed tubers (see chapters 1 & 5).

Apart from the time in a patch we might expect that social foraging also impinges on the movement between patches. In chapter 3 we focussed on movements that were not related to social interactions, which constitutes 76% of all inter-patch movements. We assumed that these movements are representative for a solitary forager and that they were predominantly a response to food density. The other 24% of recorded movements were the basis for an analysis on the effect of social interactions on the length of inter-patch
movements (chapter 4). In line with the social hierarchy we observed that singletons were more often chased away from patches than paired swans or swans that are part of a family. A swan that was chased away from a patch moved a longer distance before it initiated exploitation of a new patch than a swan that voluntarily left a patch; moreover, this displacement was greater for subordinate than for paired swans. One possible explanation for the longer movements of singletons is that this enables them to remain at the front edge of the flock where resources are unexploited (Prop & Loonen 1989; Stahl et al. 2001; chapter 4). In this line of reasoning it would be interesting to see how the movements of foragers with different social rankings are related to the position of conspecifics, and the position within the flock (see e.g. Rowcliffe et al. 2004).

The role of spatial heterogeneity in the abundance of food at stopover sites for a migratory bird

What is the significance of small-scale spatial heterogeneity in the abundance of food for a migrating Bewick’s swan? In general we can state that heterogeneity provides an opportunity for an animal to bias foraging effort to area that is rich in food, which is related to a higher gain rate (Valone & Brown 1989; Schmidt & Brown 1996). In general, heterogeneity in the abundance of food is thought to be beneficial for a forager (Sparrow 1999). Tufted ducks Aythya fuligula diving for benthic prey provide one of the few examples where an animal is not capable of taking advantage of spatial heterogeneity (De Leeuw 1999). These ducks achieved lower intake rates when Zebra mussels Dreissena polymorpha were distributed in tight clumps than when distributed more homogeneously. In the previous paragraphs I pointed out how a forager can enhance its gain rate by regulating the time in a patch or the movement in between patches. For the pondweed-feeding Bewick’s swans, which are limited by the available feeding time (Nolet & Klaassen 2005), an enhanced gain rate would result in a higher daily metabolizable energy intake.

Correspondingly, heterogeneity in the distribution of food at a stopover site would mean that higher fuelling rates can be achieved, which in turn can be translated into an increased speed of migration (figure 5; Hedenström & Alerstam 1998). In particular, in the light of the strong competition between swans we could imagine that it is crucial for a migrating swan to take advantage of the opportunity to enhance gain rates and thus migration speed to get ahead of its competitors at the next site.

Heterogeneity in the abundance of food and responses of foragers to this heterogeneity seem to be very common in natural ecosystems. Therefore, a better question to ask in this context might be ‘what would be the effect on swans if heterogeneity would disappear, i.e. if the environment would become homogeneous?’ Obviously, it would make life, or at least the migratory period, much more demanding for the swans since they would be confronted with decreased gain rates and thus reduced migration speeds (figure 5). If food was homogeneously distributed swans would fail to achieve the intake rates that we observe in
the field. Given the dependence of swans on Fennel pondweed and the very tight time window for successful reproduction we could even imagine that absence of heterogeneity could negatively affect the reproduction of swans, and consequently the viability of the population (Fryxell et al. 2005). In a homogeneous world swans would arrive too late or with too few energy stores to breed successfully, particularly in years with low food densities. Different studies on geese demonstrated that the body condition realized during migratory stopover has pronounced effects on the probability of successful reproduction (Ebbinge & Spaans 1995; Drent et al. 2003).

**Figure 5** Power required for flapping flight (W) in relation to the flight speed (m/s), for a Bewick’s swan with a mass of 6.05 kg, a wing span of 1.92 m, and a body drag coefficient of 0.1 (calculations according to Pennycuick 1975). The maximum speed of migration ($V_m$) can be found by drawing the tangent from the rate of fuel deposition (plotted on the downwards extended ordinate) to the power curve. Two scenarios are depicted. Scenario $A$ represents the natural situation observed in the Lauwersmeer in 2003, i.e. a heterogeneous food distribution (see chapter 3). The rate of fuel deposition ($99$ W) was extrapolated from Daily Energy Expenditure (DEE: $3 \cdot 10^6$ J/day) and Metabolizable Energy Intake (MEI: $12 \cdot 10^6$ J/d) observed in 1995-1996 (Nolet & Klaassen 2005). Scenario $B$ represents the hypothetical situation where the same amount of food is homogeneously distributed, which is expected to be linked with a lower deposition rate. A doubled deposition rate implies a 67% advantage in overall migratory speed. This figure is based on Hedenström & Alerstam (1998).
A scenario in which food is homogeneously distributed throughout the environment seems unrealistic (Sparrow 1999; Wiens 2000), but raises the question how heterogeneity is maintained in a system. In chapter 6 we explored how heterogeneity in the abundance of pondweed tuber biomass developed throughout the year to determine how the three most important biological processes (growth of plants, predation by swans and winter mortality) affect heterogeneity. The novelty of this study was that we distinguished between different forms of heterogeneity: spatial variance and spatial pattern (see also chapter 1). It appeared that the degree of variance and pattern strongly fluctuated throughout the year, although not in a similar fashion, but rather independently. The effect of a biological process on variance could be very different from, and even opposed to, the effect on pattern (chapter 6)! Consequently, the fact that swans meet a heterogeneous rather than a homogeneous food distribution in autumn is not the result of a single biological process. If spatial variance is enhanced by the foraging activities of swans, we would expect that exclusion of feeding swans from an area would tend to homogenize the food distribution. Spatial pattern is in fact not enhanced by the foraging activities of swans. After the foraging episode by the swans, the underlying tuber distribution pattern had even disappeared from the system (chapter 6). After the winter spatial pattern in the distribution of tuber densities re-occurred again, indicating that pattern is enhanced by winter mortality. The observation that exploitation decreases the degree of spatial pattern is not a general one. Adler et al. (2001) reviewed the effects of grazers on spatial pattern in the vegetation and concluded that foraging causes decreases in spatial pattern in some cases, but increases in others.

**Calculating the carrying capacity of a site in relation to small scale spatial heterogeneity**

The number of birds that can be supported by a site has been termed the site’s carrying capacity, and can be expressed as the maximum number of bird-days or as the maximum number of birds. Here I consider carrying capacity as an energetic rather than a demographic concept, thus I will focus on carrying capacity expressed in bird-days (De Leeuw 1997; Van Gils et al. 2004). The carrying capacity is an important tool for management decisions since it establishes the conservation value of a site. In essence, the site’s carrying capacity is determined by the amount of food on offer and by the rate at which food is consumed. The carrying capacity of a site that has 6,000,000 units of food available (Zwarts et al. 1992) equals 60,000 bird-days when a bird consumes 100 food items per day, or 30,000 bird-days when a bird consumes 200 food items per day (I here assumed that all food items are eaten, i.e. GUD=0).

To calculate the number of bird days it is important to know the forager’s currency, i.e. whether the forager maximizes daily intake or whether it satisfies daily requirements (Nolet et al. submitted). This can be illustrated by considering the effect of social interference on the carrying capacity. Social interference between foragers lowers food intake rates, at least
for subordinate birds (Vahl et al. 2005). A lower intake rate for satisfiers implies that they need more time on a day to accumulate their daily energy requirements. However, the number of bird days the site can sustain remains unchanged. For rate-maximizers a lower intake rate implies that less food is consumed during a day (maximizers continue foraging when daily requirements are met), which leaves more food that can be consumed on other days. Consequently, lower intake rates increases the number of bird-days for rate-maximizers!

There has been some debate about whether we need multi-patch models that incorporate spatial heterogeneity in the site’s characteristics to calculate carrying capacity, or that we can use a simpler one-patch model that assumes a homogeneous environment (Goss-Custard et al. 2003; Van Gils et al. 2004). Van Gils et al. (2004) advocate that multi-patch models are needed to improve carrying capacity predictions when patches differ in fitness costs of foraging (i.e. metabolic and predation costs) or in availability (i.e. time exposed to foragers). Goss-Custard et al. (2003) compared predictions of a one-patch model and a more complex spatial depletion model in which different patches are treated separately, and concluded that model predictions are often the same, even tough initial food densities varies between patches. From these studies we might get the impression that spatial heterogeneity in the abundance of food does not affect carrying capacity calculations, as long as patches are equal in fitness costs or temporal availability. In the next paragraph I will point out that this is not always true.

I consider the case that the carrying capacity is calculated from initial food density $D_i$, the critical density $D_c$ at which patches are left, and the forager’s functional response. For simplicity I assume that the environment is homogeneous in foraging costs and availability of patches, and that the forager is a rate-maximizer that feeds all day long. The environment consists of only 2 patches, each measuring 1 m$^2$. I consider two models. The one-patch type model (OPM) assumes that both patches contain the same $D_i$ which equals the average initial density for the two patches $\bar{D_i}$. The multi-patch type model (MPM) recognizes that the two patches differ in initial food density ($D_{i,1}$ and $D_{i,2}$). In this example patch 1 can contain less food than patch 2. See figure 6 for four different environments that are equal in $ar{D_i}$, but differ in initial densities in patches 1 and 2. Environment A is homogeneous: for both patches $D_i=30$ g/m$^2$. Environments B-D are heterogeneous: the smallest difference in food density is observed for environment B, and the largest difference for environment D. For the OPM the carrying capacity $C$ expressed in bird days, is calculated by:

$$C_{OPM} = 2 \cdot t_\phi$$

where $t_\phi$ is the feeding time required to deplete a patch from $\bar{D_i}$ to $D_c$ ($t$ is expressed in days). For the MPM carrying capacity is calculated by:

$$C_{MPM} = t_{\phi,1} + t_{\phi,2}$$
where $t_{\phi,1}$ is the time required to deplete patch 1 from $D_{i,1}$ to $D_c$, and $t_{\phi,2}$ is the time required to deplete patch 2 from $D_{i,2}$ to $D_c$. The forager has a type I functional response with a slope of 0.41, i.e. it takes a forager exactly 1 day to exploit a patch with $D=30$ g/m$^2$ down to $D_c=20$ g/m$^2$.

In table 2 $C_{OPM}$ and $C_{MPM}$ are presented for the environments that only differ in the variation in the initial food densities. The OPM only correctly calculated carrying capacity for environment A (no variation in initial food densities). In other words, in this example it is important to consider spatial variance in initial food densities to calculate carrying capacity. This is the result of two effects. Firstly, the rate at which food is consumed is different for heterogeneous than for homogeneous environments. The average rate at which food is consumed is an increasing function of the level of heterogeneity in the abundance of food (table 2), because food intake rate is an increasing function of food density. This explains why $C_{MPM}$ is lower for environment B than for environment A (remember that for rate-maximizers carrying capacity is lower if food is consumed at a higher rate). Secondly, the harvestable food supply, i.e. the total amount of food that can be harvested from an environment, is different for heterogeneous than for homogeneous environments. Harvestable food supply is higher for environments C and D than for environments A and B (table 2), which is caused by the fact that in environments C and D the initial density in patch 1 is already less than the GUD. This effect was not detected in the model of Goss-

**Figure 6** Schematic representations of four simple environments (A-D) that consist of two patches. The average food density in all environments is 30 g/m$^2$. Environments differ in the degree of spatial heterogeneity (spatial variance). Environment A is homogeneous, i.e. both patches contain 30 g/m$^2$. Environments B-C are heterogeneous, i.e. the food density in patch 1 is lower than the food density in patch 2, in which B is slightly, C is intermediately, and D is strongly heterogeneous. The horizontal line depicts a hypothetical critical food density threshold of 20 g/m$^2$ at which patches are left by the forager. See table 3 for the amount of biomass that is available to the forager (dark gray) and the average time a forager needs to exploit 1 g of biomass, for these different environments.
Table 2 Carrying capacity, expressed in number of bird days, four environments (A-D) that are equal in the average food density (30 g/m²) but differ in the degree of spatial variance in the abundance of food (see figure 6 for corresponding examples). The carrying capacity is calculated by a one-patch type model (OPM) that assumes that the environment is homogeneous and a multi-patch type model (MPM) that acknowledges that initial food densities vary. Furthermore, the harvestable amount of food (food that is above a critical threshold density of 20 g/m²) and the average time a forager would need to harvest 1 g of food, is presented. The average time to harvest 1 g of biomass (in days) is calculated by dividing the time required to forage the available amount of food by the available amount of food.

<table>
<thead>
<tr>
<th>Environment</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carrying capacity according to OPM (d)</td>
<td>2.0</td>
<td>2.0</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Carrying capacity according to MPM (d)</td>
<td>2.0</td>
<td>1.7</td>
<td>2.3</td>
<td>2.7</td>
</tr>
<tr>
<td>Harvestable amount of biomass (g)</td>
<td>20</td>
<td>20</td>
<td>30</td>
<td>40</td>
</tr>
<tr>
<td>Time to harvest 1 g of biomass (d)</td>
<td>0.10</td>
<td>0.09</td>
<td>0.08</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Custard et al. (2003) since the initial food density in a patch was always higher than the GUDs they employed. The larger harvestable food supplies for environments C and D explain why $C_{MPM}$ for these environments is larger than $C_{OPM}$ of environments A and B.

In the light of the abovementioned effects of spatial heterogeneity on carrying capacity calculations, we can ask the question whether acknowledgement of heterogeneity in pondweed abundance is required for carrying capacity calculations in the Bewick’s swan-Fennel pondweed study system. Firstly, only in 3% of the patches is the initial density lower than the threshold density (own data, here we assume a fixed threshold density, see paragraph on ‘regulating time in patches’). Consequently, the effect of ignoring small scale heterogeneity in the determination of the harvestable food supply is negligible. Secondly, a swan needs on average 46 s to harvest 1 g of pondweed biomass, both if food is distributed heterogeneously (field situation) and if food is distributed homogeneously (hypothetical situation) (own data, given a functional response cf. Nolet et al. 2002). This is explained by the high intake rates at high densities are in this case outweighed by low intake rates at low densities (densities lower than the average density but higher than GUD). In this specific case, the effect of spatial variance on the rate at which food is consumed is negligible. Consequently, for a pondweed bed that is homogeneous in foraging costs we do not have to acknowledge spatial heterogeneity to calculate the number of bird-days from the average initial pondweed biomass, the GUD employed by swans, and the swan’s functional response. However before we could draw this conclusion we needed to have a sound idea about spatial heterogeneity in the abundance of food in the system.
The level of spatial variance that is observed is a function of the scale at which food densities are determined (see chapter 1, Kotliar & Wiens 1990; Levin 1992). Consequently it is important to measure food density at a scale appropriate to the forager, which is normally the foraging scale or grain, which is the smallest scale at which an animal can respond to heterogeneity (Kotliar & Wiens 1990). In chapter 7 we showed in a laboratory experiment that Mallards are limited in their response to spatial variance by the scale at which heterogeneity is present. This corroborated the existence of a foraging scale. In Mallard the foraging scale is presumably related to the morphology of the bill tip (chapter 7). Bewick’s swans dig craters to loosen pondweed tubers, which makes it impossible to respond to heterogeneity at a smaller scale than the size of a crater. Consequently, the foraging scale of Bewick’s swans seems to be determined by their foraging behaviour rather than the size of their foraging apparatus.

Conclusion
The arrival of Bewick’s swans at a staging site is an impressive sight. After a period of favourable weather conditions the swans suddenly arrive in large numbers. The hundreds of vigorously calling swans turn the silent lake into a vivid white field. The intensity with which the swans plough through the pondweed bed gives the impression that they are not at ease but work hard to achieve their goals. In the light of the strong exploitative competition between swans this impression might be very right. Migration seems to be a game in which optimal decisions depend on the decisions of conspecifics. In this game it is of uttermost importance for a swan not to end up in the rear of the population but to remain in the leading front. Otherwise the swan is confronted with depleted pondweed beds at stopover sites, which ultimately inhibits successful reproduction (in spring) or risks of a freeze-over (in autumn).

Consequently, it is expected that the swans take advantage of every opportunity to enhance their energy gain rate at a site. Such opportunity is provided by the small-scale heterogeneity in the abundance of food. Therefore it does not come as a surprise that swans indeed enhance their gain rate by regulating the time they spend in patches and the movement pattern between patches, as shown in different chapters in this thesis. Although we now have a relatively good understanding of the way in which swans exploit pondweed at the local level, some details remain to be assessed. For example, it is not completely clear how swans decide to leave a patch, in particular given the fact that they forage in flocks: we have been unable to quantify to what extent swans rely on or use public information. Furthermore it is unclear how swans distribute themselves throughout a pondweed bed, and whether this is controlled by exploitative competition or social interference.

It is my conviction that it is important to understand the rules governing the time swans spend in patches and the way swans move in between patches in great detail (i.e. at a small
general discussion

spatial and temporal resolution) to understand processes that act at much larger scales, such as use of the flyway in swan migration. The challenge is to build on our understanding of the individual swan, to bridge the gap between individual behaviour and lifetime performance (a combination of survival and reproductive output). Is the success of an individual swan related to its foraging performance? The Bewick’s swan is a long-lived species and individuals can be recognized from neck-collars or coloured leg-bands. Furthermore, body condition, as a reflection of foraging performance, can be estimated in the field by observing the abdominal profile (API; see Bowler 1994). This provides a unique opportunity to relate individual variation in foraging behaviour to survival and reproductive success. Not that this will be a simple task! Such study not only requires a meticulous description of the foraging behaviour of a large number of individually marked birds, but also a detailed picture of their whereabouts and a reliable estimate about survival and reproduction allowing estimation of the fitness correlates associated with the observed foraging decisions. However, new technologies (e.g. satellite transmitters and recently applied GPS-loggers) and the devotion of a growing number of ring-reading amateur ornithologists might soon bring this within our scope.