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## Foraging in a spatially patterned world

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## Summary

The gathering of food is an important aspect of an animal's life. When food is harvested at a higher rate, a fixed amount of food is collected in less time, leaving more time for alternative activities (e.g. searching for mates), or more food is collected in a fixed amount of time, allowing a forager to assemble (more) energy resources (e.g. to prepare for a migratory journey). In many circumstances it is thus beneficial for a forager to collect food at a higher rate.

Heterogeneity in the abundance of food provides a forager an opportunity to bias foraging effort towards area that is on average richer in food, and thus to enhance food intake rate. However, this might not be a simple task since in many natural situations food items are cryptic, for example because they are buried in the sediment, and consequently the content of patches is not obvious prior to exploitation. We see a patch as the smallest discrete spatial entity of the environment encountered/perceived by the forager or as the spatial entity that is exploited during the time the forager does not move (also called a foraging station).

The central research theme in this thesis is how animals should forage in order to maximize their food intake rate in an environment that is heterogeneous in the abundance of cryptic food items. In particular, we ask how long foragers should stay in patches and how foragers should move between patches. We distinguish between two different forms of heterogeneity: spatial variance, the frequency distribution of densities, and spatial pattern, the spatial distribution of densities. Inspired by the pioneering work of Mennobart van Eerden and co-workers we choose the migratory Bewick's swan *Cygnus columbianus bewickii* feeding on buried Fennel pondweed *Potamogeton pectinatus* tubers as the main study system.

Bewick's swans dig craters to reach the buried tubers. Consequently, their foraging path is an alternation between feeding in patches (craters) and movements between patches. A forager that does not know the exact location of rich patches, but that knows the spatial pattern of the food distribution, for example because it learned this during earlier visits, can achieve a higher intake rate by regulating the length of movements between patches. In **chapter 2** we determined the optimal movement rule (i.e. the rule that maximizes long-term intake rate), for such incompletely informed forager that has prior knowledge about the spatial configuration/arrangement of food items (called a Bayesian assessor), for environments with different spatial patterns in the food distribution (clumped, random, and regular).

By comparing the best performance of the Bayesian forager with the performance of foragers that are uninformed (ignorant forager) and fully informed (prescient forager) about the content of patches, we could establish in which food distributions prior knowledge about

spatial pattern is beneficial to a forager. In most clumped and regular distributions there is a benefit of assessment, i.e. Bayesian assessors achieve substantially higher intake rates than ignorant foragers.

However, both in environments with a less strong spatial pattern and in environments that are very rich or very poor in food, the assessor did not achieve a higher gain rate than the ignorant forager. In these environments there is no benefit of assessment despite the presence of spatial pattern. In environments with a less strong spatial pattern and in very poor environments the information about the content of nearby patches is valueless due to high unpredictability in the distribution of food items. In very rich environments there is not much to gain from a sophisticated movement rule, since already the ignorant strategy achieves a gain rate close to the maximum achievable rate (prescient forager). In other words, in rich environments there is no penalty of ignorance.

In **chapter 3** we return to our specific example of an incompletely informed forager moving in a spatially patterned food distribution: Bewick's swans feeding on Fennel pondweed tubers. Pondweed tuber biomass densities appeared to be distributed in a clumped fashion, i.e. biomass densities showed a positive spatial auto-correlation at a short ( $< 3$  m), but not at a larger distance (3-8 m). We used the model introduced in chapter 2 to establish quantitative predictions about the optimal lengths of inter-patch movements of swans for this spatial pattern. A swan that moves to the patch with the highest gain rate was predicted to move to the adjacent patch (at 1 m) if the food density in the current patch had been high ( $>25$  g/m<sup>2</sup>) and to a more distant patch (at 7-8 m) if the food density in the current patch had been low ( $<25$  g/m<sup>2</sup>). These predictions were tested in the field by measuring lengths of inter-patch movements in plots where the abundance of food was manipulated experimentally by removing aboveground biomass at different stages during the growing season.

Swans regulated the time in patches, which is a response to spatial variance. Swans consume more food from rich than from poor patches, which indicates that swans harvest patches down to a constant quitting harvest rate. Moreover, in accordance with our predictions, swans responded to spatial pattern and moved a long distance ( $>3$ m) from a low density patch and a short distance ( $<3$ m) from a high density patch. The result of this strategic movement is that the frequency in which a forager encounters high-density patches is higher than the frequency in which high-density patches occur throughout the environment. Consequently swans achieve a 38% higher long-term intake rate.

The movement pattern (foraging path) is thus a reflection of the spatial pattern in the distribution of tuber densities and can be understood from an optimal foraging perspective. However this is not the complete story. Swans are gregarious and individuals frequently interact about foraging patches. In chapter 3 we only considered inter-patch movements that were not related to social interactions (76% of all movements) because we were interested in the response of swans to spatial pattern. In **chapter 4** we focus on the

remaining 24% of inter-patch movements and studied how social interactions affect the length of inter-patch movements. A swan that was chased away from a patch moved a significantly larger distance before it started to exploit a new patch than when it chose to leave the patch by itself. Individual swans differed in their dominance rank which was related to the swan's social status, in which families are dominant over pairs and singletons, and pairs are dominant over singletons. Singletons more often retreated from patches than paired swans and families, and thus social interactions had the largest influence on the foraging path of singletons. Because it is thought that longer movements deteriorate the efficiency in which high-density patches are encountered, we expect that singletons consequently achieve the lowest intake rates. However singletons might partly compensate for more frequent retreats from patches by moving larger distances to arrive at the front edge of a flock where they encounter unexploited resources.

In **chapter 5** we had a closer look at how social foraging affected patch residence times. Swans forage in groups and thus compete for food by exploiting patches. We modelled the decision 'when to leave a patch' for solitary feeding swans and swans feeding in a flock under exploitative competition. Model swans continuously update their expectation about the quality of the environment, and thus could keep track of changes in food abundance. Patches were left as soon as the intake rate in the patch dropped to the average intake rate that could be achieved in the whole environment. Since the food distribution is more or less stable for the solitary forager, it was predicted to leave patches at a fixed threshold. In contrast, a swan foraging in a group was predicted to leave patches at a flexible threshold since the abundance of food in the environment progressively decreases over time. Game simulations confirmed that model swans that leave patches at a flexible threshold were superior to swans that leave patches at a fixed threshold. Very different exploitation patterns were predicted if swans foraged with a fixed or flexible threshold. Surprisingly, the exploitation pattern observed in the field matched best with our predictions for swans foraging with a fixed threshold! Swans might be constrained to behave optimally in this respect, for example due to social behaviour or due to the (vertical) depth-distribution of tuber biomasses.

In many natural situations, food items are cryptic to foragers. Consequently, a forager needs time to assess the content of a patch, before it can respond to it. In such case knowledge about the spatial pattern in the distribution of food might be beneficial since this gives a forager a better estimate of the content of surrounding patches prior to foraging, which enhances the assessment of the content of a patch. We investigated whether a forager uses (pre-harvest) information about spatial pattern to enhance patch assessment (in addition to adjustment of its movement rule) in an experiment with Mallard *Anas platyrhynchos* foraging in environments with random, regular, and clumped configurations of full and empty patches (**chapter 8**). An assessment model was used to predict the time a Mallard would spend in an empty patch, given that the previous patch had been full or

empty, for the different spatial distributions used in the experiment. Consistent with predictions, in the clumped distribution Mallard spent less time in an empty patch if the neighbouring patch had been empty than if it had been full. This effect was not observed for the random distribution. This shows that Mallard use pre-harvest information on spatial pattern to improve patch assessment. (Patch assessment could not be evaluated for the regular distribution).

In this experiment Mallard surprisingly did not respond to spatial pattern by regulating the length of their inter-patch movements, but virtually always moved to a neighbouring patch. An explanation for the result that pre-harvest information on spatial pattern affected patch assessment and not movement is that Mallard move to the nearest patch where the expected intake rate is higher than the critical value, rather than to the patch where the highest intake rate is expected.

Foragers can lift their long-term intake rate by regulating the length of inter-patch movements and time in patches, as illustrated above for the Bewick's swan feeding on Fennel pondweed. Therefore, heterogeneity in the abundance of food is considered to be, in most cases, beneficial for a forager. As such foragers eat more from high than from low density patches, the question arises how spatial heterogeneity is maintained.

In **chapter 6** we investigated how spatial heterogeneity in the abundance of Fennel pondweed tubers developed throughout the year, with the novelty that we distinguished between spatial variance and spatial pattern. We identified three important processes in the pondweed's life cycle: plant growth (summer), swan foraging (autumn), and winter loss (winter). Since we sampled tuber biomass densities after each period we could assess the effect of each process on variance and pattern in isolation. Surprisingly, variance and pattern appeared to have their own temporal dynamics and the effect of a process on variance could be very different from the effect on pattern. Spatial variance was mostly enhanced by swan grazing whereas plant growth strongly reduced the degree of variance in the system (but could not wipe it out). Spatial pattern had disappeared after the foraging activities of swans but had re-appeared again after winter losses. We concluded that variance and pattern are maintained by different biological processes, and that it is important to distinguish between these different forms of heterogeneity when trying to understand the functioning of an ecosystem.

An important assumption in these studies on foraging in heterogeneous environments is that the foragers are able to respond to heterogeneity. However, the heterogeneity a forager perceives depends on the scale of the food distribution and the scale at which the forager samples the environment. This concept was investigated in a laboratory experiment with Mallard (**chapter 7**). We recorded search patterns of Mallard feeding on cryptic prey in differently scaled food distributions. A small magnet attached to the lower mandible allowed

us to record the position of the duck's bill in great detail in a feeding tray that was underlain by magnet sensors. Ducks responded to heterogeneity by allocating more time to full than to empty cells, but only when the size of the cells was larger than 2x2 cm, which corroborates the existence of a foraging scale, i.e. a limit below which a forager cannot respond to existing heterogeneity. A response to heterogeneity was linked to a higher food intake rate, thus a forager benefits from the ability to subdivide the environment into profitable and non-profitable areas. At large scaled distributions Mallards responded to a food capture by an area-restricted search. However, we argue that partitioning the environment at the foraging scale in itself could be a mechanism to concentrate foraging efforts within profitable areas, because Mallard were able to respond to heterogeneity even without conducting area restricted search.

In the general discussion (**chapter 9**) we viewed our study system at a much wider spatial scale: the scale of the swans' flyway. We recognized that swans have an extremely tight time window for successful reproduction: the frost-free period at their sub-arctic breeding grounds lasts only about 120 days, whereas they need about 110 days to complete their breeding cycle. Consequently it is important for swans to arrive on time at their breeding grounds, and presumably also to arrive with some surplus energy reserves that can be used to prepare eggs and incubate them. Heterogeneity in the abundance of pondweed tuber densities allows a Bewick's swan to substantially enhance their food intake rate by regulating time in and movement between patches, and thus to increase fuelling rates (energy deposition rates) at stopover sites. For the Bewick's swan a doubled deposition rate implies a 67% advantage in the overall migration speed! Given the strong dependence of Bewick's swans on Fennel pondweed and the very short time window for successful reproduction we could imagine that absence of heterogeneity could preclude swans to reproduce successfully, especially in years with low initial tuber biomass densities at stopover sites, and thus strongly negatively affects the viability of the population.