SYMP09: Integrating the concept of spatial heterogeneity in ornithological theory and practice

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After ignoring spatial heterogeneity in the 1960s and 1970s, ecologists have become aware that the concept of heterogeneity cannot be ignored in ecological theory if it is to explain or predict patterns and processes in the real world (LEVIN 1992 – Ecology 73, 1943–1967; SPARROW 1999 – Trends in Ecology and Evolution 14, 422–423; TILMAN & KAREIVA 1997 – Princeton University Press). In the proposed symposium examples are presented on how the explicit incorporation of spatial variation improves the understanding of the behaviour of birds. Topics that are presented are mate choice, intraseasonal iteroparity, and foraging behaviour during the breeding and migratory season.

SYMP09-1 Mate choice in a patchy world

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Existing models of mate choice assume that potential mates are distributed regularly in a homogenous environment. We model an environment in which males are distributed in clusters, e.g. on „islands" of suitable habitat or on leks. We assume that mate finding and inspection is costly in terms of time and survival, and that it is cheaper for the female to inspect another male within the current patch than to travel between patches. If females can remember the position and quality of the best male so far inspected, and can later return to males in the same patch at no cost, a simple two-threshold tactic of mate choice is optimal. The female compares each male versus one fixed threshold quality and mates if his quality is sufficient. If all males in a patch turn out to be of insufficient quality, she lowers the threshold; if the quality of the best male now meets this new criterion she returns to mate, otherwise she moves to a new patch. The model predicts that only the value of the second threshold depends on the spatial structure of the environment. We perform sensitivity analyses to examine the effect of changing model parameters such as distance between patches and patch size, inspection cost, variance in male quality, etc. We also determine optimal strategies when (1) there are recall costs, when (2) the last males in a patch are harder to find, and when (3) the quality distribution of males varies from patch to patch or from year to year, so that females must learn the population mean quality from their sampling. The optimal strategies of mate choice in condition (3) depend on several variables and are cognitively quite demanding. However, the simple two-fixed-threshold rule still performs very well, as do various simplifications of it, such as only using the end-of-patch threshold. We also investigate performance of other heuristics of choice proposed in the literature, such as best-of-n and sequential search rules. We argue that incorporation of a patch structure into mate choice models is not only more realistic but also allows us to explain some aspects of the complex mate choice tactics that have been found in empirical studies of birds.

SYMP09-2 Habitat-specific differences in the level of intraseasonal iteroparity in great tits breeding in heterogeneous environment

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Recently, habitat heterogeneity has captured serious attention in population and conservation biology. Great tits prefer deciduous forests as breeding habitats. However, they are able to reproduce in managed pine forests as well when nest boxes are provided there. In 1999–2002, we measured various breeding parameters of the great tits breeding in a heterogeneous habitat complex consisting of deciduous woodland patches and pine forests. In the pine forests, total number of eggs laid during a season was divided more equally between two successive breeding attempts than in the deciduous forests where substantial part of the eggs were laid during the first breeding attempt. As a result, in the deciduous forests the young that fledged during the second breeding attempt was significantly heavier and with longer tarsi than the young that fledged during the first breeding attempt, while no such seasonal increase in fledgling quality was observed in pine forests. We suggest that intraseasonal iteroparity plays an important role in optimising breeding tactics of great tits in different habitats. The possible role of various proximate and ultimate factors (e.g., food dynamics, micronutrient limitation, predation risk) in maintaining above habitat-specific differences will be discussed.

SYMP09-3 Spatially explicit habitat selection by central place foraging white storks

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White storks, like many birds, live in a patchy environment, with good habitat patches dispersed. When they have nestlings they often need to travel long distances to collect food for the young. While traveling they may incur both indirect costs in terms of the time they spend flying back and forth to the nest, and direct in terms of increased wear, stress and possibly predation or accident risk. The way in which these costs are weighed by the storks will influence how large a travel cost an individual is willing to take, in order to get a certain benefit. Habitat patches of different qualities give the storks different expected benefits. The result is a decelerating relation between habitat quality and maximum travel distance. However, this relation is state-dependent, and hence depends on overall environmental quality. Based on this, I will present a model for spatial explicit habitat selection. The model is developed with special reference to the white stork, but should be general for most animals living under similar circumstances.

SYMP09-4 Small home ranges vs. roaming during migratory stopovers of small passerines: is foraging ecology responsible?

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Some passerines are known to remain within rather small home ranges during their migratory stopovers. A closer examination shows that small home ranges (that sometimes, but not always, are defended territories) are typical of individuals that have established themselves at a stopover site, remain for several, typically more than 1–2 days, and are refuelling. This has been demonstrated for e.g. European robins and wrens by analysing their captures and recaptures in a standardised mist-netting project at Rybachy (Courish Spit, Russia). For the European robin, this finding was confirmed by radiotracking migrants during stopovers on spring and autumn passage. On the other hand, other species, e.g. reed and sedge warblers and blackcaps, move rather broadly at stopovers, several individuals sharing the same area. It is assumed that differential pattern of using space during stopovers is related to different distribution (more or less uniform vs. patchy) of the main food consumed by the species in question. This means that the same area may be strongly heterogeneous and comparatively homogeneous for the birds of the same size class (e.g. sedge warblers and European robins). It has some implications when several avian species are included in the analysis of spatial heterogeneity.

SYMP09-5 Foraging by swans in a continuous, heterogeneous environment

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A forager faces two basic problems when foraging in a certain area on a certain prey type: (1) When to leave a foraging spot? (2) How to move between foraging spots?
Most research on foraging decisions focusses on the first problem. Movement between foraging spots is assumed to be random, which is a mathematically convenient, but biologically unrealistic assumption. We studied bewick's swans foraging on below-ground tubers of fennel pondweed (after the above-ground plant matter had disappeared). Because a pondweed field is a non-discrete environment, it is not possible to define foraging spots (patches) beforehand. We measured both the movement patterns of the swan and the spatial distribution of the tubers on two different scales. We show that foraging is an alternation between a feeding and a searching mode. As a result of this distinction we were able to define patches a posteriori and determine searching behaviour between patches. Searching behaviour of bewick's swans probably takes place at multiple scales. The searching patterns are probably related to the spatial distribution of the food items. Small scale search paths are not random, but area-restricted with the swans tending to remain within a certain, presumably profitable area. Large scale search paths are also not random but directional, and probably represent an efficient way to find new profitable areas.

SYMP09-6 Decision-making by red knots feeding in a heterogeneous, intertidal environment

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In an intertidal environment foraging options change continuously due to the temporal coverage of potential food sites by the tide. Aiming to understand how red knots (*Calidris canutus*) cope with

this problem, we (automatically) tracked radio-marked individuals during their daily foraging trips in the Dutch western Wadden Sea. In order to quantify the foraging benefits throughout their environment, we sampled available prey densities at more than 2,500 sites (in a fixed grid at 250 m intervals). These prey densities were translated into potential intake rates using experimentally determined functional response parameters and estimates per individual bird of digestive processing capacity. This latter measure was obtained by ultrasonographically estimating the size of each bird's gizzard. Using dynamic programming, we predicted for each individual the optimal foraging pathway and compared these to the actual data.