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Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns

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ABSTRACT

Animals interact with their habitat in a manner which involves both negative and positive feedback mechanisms. We apply a specific modeling approach, "multi-scaled random walk", for the scenario where a spatially explicit positive feedback process emerges from a combination of a spatial memory-dependent tendency to return to familiar patches and a consequently objective or subjective improvement of the quality of these patches (habitat auto-facilitation). In addition to the potential for local resource improvement from physically altering a patch, primarily known from the ecology of grazing ungulates, auto-facilitation from site fidelity may also embed more subtle subjective, individual-specific advantages from patch familiarity. Under the condition of resource superabundance, fitness gain from intra-home range patch fidelity creates a self-reinforcing use of the preferred patches on expense of a broader foraging in *a priori* equally favorable patches. Through this process, our simulations show that a spatially fractal dispersion of accumulated locations of the individual will emerge under the given model assumptions. Based on a conjecture that intra-home range patch fidelity depends on spatial memory we apply the multi-scaled random walk model to construct a spatially explicit habitat suitability parameter H_{ij}, which quantifies the dispersion of the generally most constraining resource from the individual's perspective. An intra-home range set of observed H-scores, H_{obs}, can then be estimated from a simple 2-scale calculation that is derived from the local dispersion of fixes. We show how the spatially explicit habitat utilization index H_{obs} not necessarily correlates positively with the local density fluctuations of fixes. The H-index solves some well-known problems from using the pattern of local densities of telemetry fixes – the classic utilization distribution – as a proxy variable for relative intra-home range habitat quality and resource selection. A pilot study on a set of telemetry fixes collected from a herd of free-ranging domestic sheep with overlapping summer home ranges illustrates how the H-index may be estimated and interpreted as a first-level approach towards a more extensive analysis of intra-home range habitat resource availability and patch preferences. Spatial memory in combination with site fidelity requires a modeling framework that explicitly describes the property of positive feedback mechanism under auto-facilitation in a spatio-temporally explicit manner.

1. Introduction

Many animals use their habitat through interplay between short-term exploratory displacements and longer term returns to previously visited patches (Börger et al., 2008; Dalziel et al., 2008; Gautestad and Mysterud, 1995, 2005, 2006, in press; Van Moorter et al., 2009; Wolf et al., 2009). Numeric simulations have shown that a multi-scaled kind of movement which includes a tendency for homing nurtures a self-reinforcing kind of preference for a subset of intra-home range patches, on expense of a broader exploitation of patches of *a priori* similar quality (Gautestad and Mysterud, 2005, 2006, in press). Return events to patches outside the individual's current field of perception imply dependence on spatial memory (reference memory), i.e., the animal makes use of a cognitive map of previous habitat experiences in a spatially explicit manner (Bailey et al., 1996). Preference for familiar sites leads to the emergence of a home range.

This kind of self-reinforcing patch use leads to system complexity which not only generates non-trivial heterogeneous patch use within the home range but also may require novel statistical protocols for applied ecology. In this paper we illustrate some of these challenges through numeric simulations, which under the given boundary conditions show shortcomings of studying the spatial variations of local telemetry fix densities as a proxy variable for local resource variations (a fix refers to a location of the individual at a specific point in time, and the set of fixes collected over a time

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period within a specified area like a virtual grid cell gives the local fix density). Our model also leads to a proposal for a novel index for the analysis of telemetry fixes with respect to the study of local resource matching and intra-home range habitat preferences.

The model illustrates the dynamic shift from a positive feedback regime under below-equilibrium conditions (resource superabundance) towards negative feedback and equilibrium condition at higher level of resource consumption. Under conditions of superabundance of heterogeneously distributed resources the model predicts a positive correlation between resource distribution and the individual's space use as measured by a local index H_{ij} over a spatial two-dimensional grid (H will be defined below), but not necessarily by the traditional index based on the local density variation of fixes (the classic spatial utilization distribution, UD). Even if there is a general positive correlation between local resource abundance and intensity of patch use as measured by local density of fixes (Bailey et al., 1996; Bennett and Tang, 2006), the latter is confounded by the home range center-periphery distance and initial chance factors linked to which patches become used in a self-reinforcing manner. The difference between the proxy variables H and UD are particularly apparent in a hypothetical homogeneous environment, where the present model predicts similar-sized H_{ij} scores, while the UD varies.

A self-reinforcing, positive feedback type of patch use may lead to fine-scaled habitat auto-facilitation. Online Appendix A1 provides a conceptual illustration of a positive/negative feedback system in the context of grazing ungulates. Habitat facilitation is normally a descriptor of how a keystone species may facilitate the habitat for other species (Arsenault and Owen-smith, 2002; Fox et al., 2003; Korpinen et al., 2008; Liess and Helmut, 2004; Pringle, 2008). However, a species like a grazing ungulate may also auto-facilitate a given habitat in a self-reinforcing manner, and thereby improve or maintain the local habitat's grazing potential for a given individual, family group, herd or local population. Mild grazing, i.e., below or at an optimum intensity of patch use, may induce a higher re-growth rate and/or maintain a high level of digestibility for some important food plants (Mobæk et al., 2009). For example, with respect to free-ranging domestic sheep browsing on seedlings and saplings of deciduous trees in a forested landscape this will over time facilitate a more open structure, with better freedom for movement and improved growth conditions for some of the sheep's major food plants. Further, sheep will quickly after being released in the early summer begin – to a larger or smaller extent – to constrain their habitat use to some patches and areas on expense of other areas with apparently *a priori* similar grazing potential, due to strategic (i.e., long-term memory-dependent) returns to previously visited locations in-between more opportunistic and exploratory movements. This behaviour opens for the common management practice to "steer" the sheep to establish home ranges in specific locations in a given landscape at the initial time of release, either by active herding in the initial phase or by strategic placement of salt stones close to the point of release.

Experiments in the field and in enclosures have confirmed that grazing ungulates under specific conditions may in fact increase local carrying capacity by grazing and browsing – i.e., a positive feedback loop – up to an optimal level of grazing pressure (Bell, 1971; Frank, 1998; McNaughton, 1976, 1984; McNaughton et al., 1997; Mysterud and Mysterud, 1999; Rhodes and Sharrow, 1990). Free-ranging ewes have also been shown to influence their lambs' future home range locations to become similar to their mother's site preferences (Lawrence, 1990). Thus, a cultural inter-generation transmission of site preferences will then take place.

In the present context we define auto-facilitation to also embed patch familiarity as such. In this case a given individual-specific patch potential improves due to revisits to this patch on expense of visits to alternative patches with *a priori* similar qualities for the individual. This kind of improved effectiveness with respect to patch use is obviously very widespread. Patch familiarity implies a potential for improved use of local food resources and other fitness-related attributes (for example, shelter and escape routes) without necessarily altering the physical structure of the respective patches. Thus, a specific patch may have a different, subjective potential for individuals that have different level of experience with this patch.

Even if local resources may improve over some range of grazing intensity, intense grazing pressure is characterized by classic negative feedback loops where Malthusian constraints will dominate the dynamics. The net fitness gain from patch familiarity obviously also has a limit. This shift from a positive to a negative feedback regime is compliant with equilibrium conditions close to carrying capacity at the local population level. The equilibrium condition represents the regime for ideal free distribution models, which predict various forms for local resource matching (including – but not limited to – the classic 1:1 match) from specific boundary conditions (Ranta et al., 2006; Treganza, 1995). At the individual level, this equilibrium state is typically modeled and analyzed under the context of intra-home range patch preference as estimated by patch quitting harvest rates (Pusenius and Schmidt, 2002). The marginal value theorem (Charnov, 1976) also describes an over-all equilibrium condition with respect to patch use.

The ecological gradient from resource superabundance to equilibrium situations with various degree of resource matching indicates that an optimum level of grazing pressure exists. Below and close to this optimum, i.e., *in a below-equilibrium system state*, positive feedback effects from habitat facilitation on local carrying capacity and individual resource matching is expected to have stronger influence than negative feedback effects (Online Appendix 1A).

Below we describe a modeling approach which explicitly describes this kind of continuum from a positive to a negative feedback situation. From this model we propose a novel index that may serve as a more realistic alternative to the classic approach for intra-home range habitat quality and preference estimates when space use is influenced by long-term memory effects, and illustrate its application from a simulation scenario.

2. The multi-scaled random walk model

The multi-scaled random walk (MRW) model (Gautestad and Mysterud, 2005, 2006, in press) builds on a statistical mechanical approach to simulate animal movements under the influence of a cognitive map (spatial memory), where exploratory steps are interrupted by goal-oriented returns – "short-cuts" – to previous locations. While a classic random walk and correlated random walk regards a low-order Markovian (i.e., autoregressive) process where memory effects on successive steps are limited to short-term influences from one or a very low number of preceding steps, the MRW with default parameter values and boundary conditions implies infinite memory or at least spanning the time period for the actual data collection. The memory allows for directed returns by the animal to previously visited patches, outside the individual's current field of perception, and rests on an assumption about a parallel processing rather than Markovian kind of implementation of spatial memory effects (Gautestad and Mysterud, in press).

The term "statistical mechanics" is important in the present context. It implies a different model approach than "mechanics". A mechanistic model typically defines a set of relatively detailed behavioral-ecological algorithms for individual behavior, which is played out in a deterministic manner within a spatial arena. The behavior may also be pseudo-deterministic, where strict movement rules are also influenced by some magnitude of statistical noise as expressed by degree of persistence in inter-step direction (feasibly implemented by a correlated random walk algorithm).