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Spatially explicit models of group foraging by herbivores: what can Agent-Based Models offer?

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Abstract – Spatially explicit models of herbivore foraging can increase the knowledge of ethologists by enabling the prediction of the evolution of complex systems and revealing underlying behavioural mechanisms. We first show how spatially explicit models that do not distinguish between individuals imply making assumptions which violate some basic biological principles. Next, we describe how the main behavioural processes that determine herbivore foraging have already been incorporated in spatially explicit individual-based models of foraging. We then discuss how the use of agent technology promotes the inclusion of social oriented cognition in individual-based simulations, emphasising the emergence of macro-phenomena from the local interactions between individual organisms. This approach makes agent-based models particularly suited to simulate the behaviour of groups of foraging herbivores. We discuss how agent-based models can help to investigate conditions that are not easily amenable to experimentation, such as the effects of differences in memory capacity or in sociability, and how they are adapted to integrate the experimentally-demonstrated laws, processes and theoretical frameworks developed in herbivore foraging.

agent-based model / grazing / individual-based model / social behaviour / spatial memory

Résumé – L'apport des systèmes multi-agents à la modélisation du pâturage des herbivores. Les modèles spatialisés relatifs au pâturage des herbivores augmentent la connaissance des éthologues lorsqu'ils permettent de comprendre les mécanismes sous-jacents au fonctionnement des systèmes, et de prédire leur évolution. Nous commençons par montrer que les modèles spatialisés qui ne prennent pas en compte les caractéristiques individuelles des animaux vont à l'encontre de principes biologiques majeurs. Puis, nous décrivons comment les principaux mécanismes comportementaux qui déterminent le comportement des herbivores au pâturage ont déjà été pris en compte dans des modèles spatialisés individus-centrés. Ensuite, nous discutons que l'approche multi-agents s'adapte remarquablement bien à la représentation du comportement de groupes d'animaux, parce qu'elle permet de représenter les conséquences d'interactions d'agents agissant en parallèle, de telle manière qu'elles influencent le comportement de l'ensemble du système. Nous montrons alors comment un modèle multi-agents peut permettre d'explorer des situations difficiles à tester expérimentalement, comme par exemple les conséquences de variations des capacités mémorielles des animaux ou de

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leur sociabilité, et l'intérêt de cette approche pour intégrer des résultats expérimentaux et des concepts dans un modèle d'utilisation d'une parcelle par un troupeau.

comportement social / mémoire spatiale / modèle individu centré / pâturage / système multi-agents

1. INTRODUCTION

Spatially explicit models are needed to represent the behaviour and impact of herbivores on heterogeneous pastures, since this is typically a complex system that combines individual, social and spatial processes with vegetation dynamics. In this paper, we review the different modelling techniques that have been applied to it, and we will focus on why the agent-oriented approach is particularly interesting for many advanced modelling goals. Indeed, research in the field of multi-agent systems and agent-based models (ABMs) is gaining in recognition because of the ability of ABMs to emulate complex systems. If a system is considered as a set of elements in interaction, a system qualified as "complicated" can be understood by decomposing it into simple elements analysable separately (reductionism). On the contrary, a system qualified as "complex" cannot be reduced to the sum of its parts (holism) [1]. Indeed, when the global system presents properties which are not directly deductible from those elements which compose it, and the information brought by elements taken in the whole are richer than those stemming from the elements taken in isolation, the global functioning of the system must be studied by simulation [34].

It is the confrontation with complex situations of a natural type (physics, biology, ecology, etc.) that instigated the first research on the notion of systemics [33, 47]. These reflections were then adapted to technological problems in various engineering fields including computer sciences. In the late nineteen-sixties, the Simula language introduced the computer notion of *object*, which slowly became a fundamental concept for information systems and which has revolu-

tionised software development techniques since the nineteen-eighties. Computer objects are passive and rapidly, the notion of computer *actor* was introduced to express the active and autonomous aspects of some objects that could also express individual variability. Then computer *agents* were introduced as a more advanced notion to take into account complex social interactions. With agent simulation, it became possible to represent environmental phenomena as the consequence of the interactions of parallel agent sets, where each agent has its own operational autonomy. This idea comes from distributed artificial intelligence and has been recently surveyed by O'Hare and Jennings [37], Ferber [23] and Odell [36]. Software agents can express social behaviour and this feature is particularly welcome when dealing with the simulation of pure social science, or with the modelling of behavioural problems [4]. Recent studies show that ABMs are increasingly used, not only for the resolution of problems and the development of software, but also to improve the understanding of complex systems by simulation [28, 35]. This is notably the case in domains in which mathematical models are not available, either because the dynamics are far from an equilibrium, or because the systems are open (creation and destruction of entities) or very heterogeneous as in the case of herbivore foraging. In some cases, conducting simulation experiments is the only way to analyse and understand the behaviour of a complex system. This is the case for instance with individual-based models (IBMs), representing social or ecological dynamics, and for which the cumulative effect of interactions can lead to unexpected effects, generally impossible to formalise analytically [15].

In addition, taking into account spatial processes is now recognised as an essential feature for ecological modelling and in particular for group foraging. However, there are still a number of models which do not take spatial effects into account, assuming that individuals have an equal effect on every other individual. Huston et al. [31] have already explained that this kind of assumption is too clumsy in many situations since a basic biological principle precisely states that interactions between individual organisms are inherently local. Ignoring that individuals are mainly affected by their neighbours was almost mandatory when the modelling tools available were limited to state-variable models and differential equations. Since the last decade and thanks to modern computer performances, it is now feasible to develop powerful stochastic discrete-event simulations on a regular desktop computer, and thus IBMs considering spatial constraints have started to be more intensively studied for ecological modelling.

In the first section of this review, we present spatially explicit models of herbivores that do not distinguish between individuals. Then, we describe how the main cognitive abilities observed in herbivores have already been incorporated in spatially explicit IBMs of herbivore foraging and how this approach makes it possible to express individual differences in physiology and behaviour in the same group. Finally, we discuss how the use of agent technology promotes the inclusion of social oriented cognition in individual-based simulations, emphasising the emergence of macro-phenomena from the local interactions between individual organisms.

2. SPATIALLY EXPLICIT MODELS OF HERBIVORE FORAGING THAT DO NOT DISTINGUISH BETWEEN INDIVIDUALS

Since spatial constraints and heterogeneity play an important role in foraging, they

have been tackled and studied with various modelling techniques. Explicit modelling of the effect of spatial heterogeneity on population dynamics is possible with a pure mathematical approach. Cantrell and Cosner [11] present such models applied to predator-prey systems at various spatial scales. These models are based on the classical reaction-diffusion theory. They are, however, very limited, since they only allow analysing behaviour under variations in patch size at equilibrium or pseudo-equilibrium. This approach requires an important effort in mathematical modelling, which is still affected by limitations since it does not consider individual differences. Applied to herbivores, Shiyomi and Tsuiiki [42] used a mathematical model with diffusion equations to investigate the spatial patterns formed by a small herd of grazing cattle. The distance between the individuals was determined by a combination of attractive and repulsive behaviour operating among individuals, together with some random movement rules. This let the model accurately predict the proximity of individuals within the group according to animal activity. The forces such as those calculated in these two models can be translated into biases to the probability of outcomes in animal decisions. Biased diffusion allows multiple search goals (e.g., foraging and social goals) and multiple-scale foraging decisions to be combined and has been used to investigate the mechanisms herbivores may use to achieve their distributions in heterogeneous environments [22].

Within the mathematical approaches, continuous models (i.e. where time is explicitly considered as continuous) often imply making strong assumptions on foraging behaviour. For example, Wallis de Vries [48], in a continuous simulation on a spatial grid, assumed that the animals had a perfect knowledge of the location of food patches and that their movements occurred via the shortest route between patches. However, depending on the modelling goals, interesting results can be obtained. This particular simulation suggested that travel costs may

be an important factor in foraging decisions, even though they constitute less than 10% of daily energy intake. It also suggested strong interactions between the abundance and spatial distribution of food patches on the searching success of herbivores. To simulate the grazing behaviour of a sheep, Baumont et al. [6] developed a mechanistic model of intake rate integrating sward structure and foraging decisions, based on the nutritional requirements and digestive processes of an animal. Satisfactory validations were obtained on data sets recorded under either rotational or continuous grazing. The choice of the grazed horizon is correctly simulated under these different management scenarios, but grazing is not spatially explicit. Pedersen et al. [39] used a discrete-time, stochastic compartment model based on difference equations with a time interval of one week to simulate the effect of sheep grazing on vegetation and a resident bird population dynamics. The spatial aspect is limited to the consideration of 15 patches in different stages of vegetation development and onto which different grazing events were applied. Sheep requirements, the number of grazing animals and a very simple diet preference function were considered to assess the impact of animals. Conversely, other variables such as fire occurrence, chick recruitment and bird mortality were considered, enabling the authors to discuss the risk of bird extinction under different management scenarios.

Regression techniques, artificial neural networks and fuzzy logic may also be applied to spatial foraging. Such modelling techniques require precise field data in order to be applied thoroughly. For instance, a spatial method originally used in human geography has been investigated for mammalian herbivore foraging [38]. Such models are named spatial interaction models and indeed they are powerful tools for describing the aggregate pattern resulting from many individual behaviour decisions. Though these models are poor in revealing the underlying mechanisms, as individual decisions are obscured by the aggregation, the

spatial pattern of vegetation defoliation by herbivores is obtained by taking into account that individual foraging decisions are influenced by the attraction of preferred patch area and by the distance, leading to a classical regression equation. Artificial neural networks require obtaining large sets of temporal series that are mandatory in the training of the model [12]. Though spatial trajectories can be predicted when a massive amount of spatial data is available, spatially explicit modelling including patches is typically not the application domain of connectionist approaches. Conversely, patch choice can be simulated by fuzzy logic [32]. Although not spatially explicit, the animal behaviour in this model is simulated by a fuzzy system which takes into account the information gathering of animals under conditions of uncertainty. The fuzzy aspects were introduced at various levels expressing the fact that animals are uncertain that they have visited the same location before and also the fact that the amount of food in a given location varies. With this approach, the complexity of natural environments is handled by a cognitive model with fuzzy sets or classes, which requires induction guided by background knowledge about the variability of the classes.

3. SPATIALLY EXPLICIT IBMS FOR HERBIVORE FORAGING: BIOLOGICAL PROCESSES AND USE IN IBMS

The survey proposed by Grimm [26] presents what has been learned with individual-based models and also in what directions future research is heading. As stated by Huston et al. [31], a number of models are based on assumptions that violate some basic biological principles. One of the main points is to avoid the description of several organisms by a single variable. Indeed, according to genetic laws and to environmental influences, individuals express differences in physiology and behaviour. Moreover, it is not biologically consistent to

assume that each individual has an equal effect on every other individual. Thus a sound approach involves taking into account both individual and spatial aspects. IBMs simulate individual organisms rather than populations. They require laborious computations and therefore only became widely available when the increase of computing power was sufficient, which occurred in the nineteen-nineties [13, 14]. In the case of herbivores, the simulation of individuals helps to obtain elementary information that can be used and recombined to help understand group behaviour.

Biological processes to consider in spatially explicit IBMs on herbivore foraging include patch selection and walking decisions that influence animal distribution in the plots. Patch selection is determined not only by preferences associated with quality and taste, but also by the cost of obtaining food. This cost modifies food intake rate and, according to the Optimal Foraging Theory, animals will select patches that maximise their energetic efficiency, i.e. their nutrient intake rate [43]. Herbivores readily associate visual cues, such as sward height, brightness and bulk density, with the presence or quality of food, and then use that information to forage efficiently. The grazing path of herbivores is relatively linear, but tortuosity and walking speed vary according to the value of the area being exploited. Within a rewarding patch, an animal will reduce walking speed and increase its rate of turning to remain within the locality, a behaviour called area-concentrated searching [8]. On a larger scale, herbivores can adequately evaluate marginal intake rates and select feeding sites and patches that maximise their energetic efficiency. Cattle [3] and sheep [19] learn food distribution and use their spatial memory to return efficiently to some areas of the plots where they find preferred food items, and this further decreases foraging costs. Experimentally, it has been observed that sheep move to the nearest patch if they are readily distinguishable and of equal value [27]. More generally, they appeared to evaluate travel dis-

tance between patches and edible biomass within patches, and equally walked to patches with similar food quantities relative to distance [20].

Roese et al. [40] developed an IBM to simulate the foraging behaviour of the moose, in which an animal is characterised in terms of physical, physiological, but also cognitive attributes without social interactions. Movements are modelled as a sequence of steps in response to perceived resources, and the animal orients itself to the food item within its perceptive field allowing the highest reward relative to distance. This simulation gave results on foraging activity and dietary choices congruent with behavioural observations, and showed that foraging efficiency in the moose varies with changes in the structural and spatial properties of resources. Turner et al. [46] also used an individual-based approach to simulate the foraging success and consequent survival chances of a herbivore in different habitats according to its movement rules. Compared to a random movement rule, the best direction rule, that minimises the distance to walk to reach food along the grazing journey, increased animal survival in simulations. Benhamou [8] determined the theoretical efficiency of area-concentrated searching using computer simulation. When foraging in habitats having the same overall food density but differing according to its distribution, an animal exhibiting optimal spatial memory-based area-concentrated searching behaviour was able to harvest three to five times more food items than if it did not exhibit any area-concentrated searching behaviour but moved in a straight line with an optimal constant speed.

Spatial memory is classically represented as a two-part code, reference and working memory. Reference memory is the map-like representation of the grazing environment. Working memory is used to remember which feeding sites have been recently grazed by the animal [3]. Consequently, modelling spatial memory must consider three main characteristics: a predefined

maximum size, an indexed search method, and ability to get, integrate, update and delete information to make room for fresh information if the data has not been consulted for a certain time. Modelling work has up to now focussed on the procedures used to make such a dynamic use of memory. In the model of Bailey et al. [3], the effects of abiotic factors (slope, distance to water, etc.) are integrated with site forage value to define a *perceived site value*. A site will be selected if its perceived value is above or approximately equal to a *reference value* calculated as the moving average of perceived site values encountered during the last four days. For each site, perceived site value decays with time to reflect that herbivores give a stronger weight to the most recent information because it is more certain. Foragers with high devaluation rates for past events can more quickly correct their estimates of patch quality as it changes. Consequently, distant past experiences have lower value in environments where the distribution of food is less predictable, and this whether patches are encountered in a random sequence [30] or, as for grazing herbivores, in a non-independent sequence [24].

4. AGENT-BASED MODELS OF GROUP FORAGING BY HERBIVORES

In an ABM, agents encapsulate and perform their individual tasks locally, but they influence the global behaviour of the system. The use of agent technology in computer simulation promotes the inclusion of social-oriented cognition into individual-based simulations, emphasising the emergence of macro-phenomena from micro-level specifications [16]. This approach has been used to study ecosystems with biological entities like fishes [45] or insects [17], or artificial entities [25]. It is also well suited to foraging herbivores because they are separate individual organisms, perform tasks in parallel and have individual actions

influencing global behaviours. Readers interested in a taxonomy of agents (deliberative, cognitive, reactive, etc.) or whatever combination of the various existing agent strategies can consult Ferber [23].

Our thinking is that the Multi-Agent System paradigm is used at its best if there is a need to simulate animal interactions and/or complex social behaviour. Since herbivores forage in groups, they can benefit from the feeding sites discovered by other members of the group, and long-distance movements of the whole herd towards a new feeding site, the water point or a location to rest are initiated by a limited number of animals called leaders [2]. On sites, herbivores face the negative effects of competition for food, and inter-individual distances therefore increase with decreasing vegetation availability. Another process to consider in spatially explicit models of herbivore foraging is social attraction that influences animal distribution in the plots. In a mosaic, an animal will move away from its group to reach a preferred feeding site located some distance away according to its sociability, the number of accompanying peers and its degree of affinity with these peers, e.g. sheep more easily split into subgroups when accompanied by several familiar peers [9].

Beecham and Farnsworth [7] first used an individual-based approach with some degree of sociability between individuals in a model developed to study foraging by herbivores in a complex environment. Optimal spacing from other animals was based on a balance between positive (e.g. protection from predators) and negative (e.g. competition for food) forces among individuals. The model showed that social interactions can constrain patch choice, which can then result in a short-term reduction of intake and a greater degree of variability in intake rate. Although one of the main interests of ABMs is that they give the opportunity to consider social and local interactions between individual organisms and their emerging properties [31], recent developments have mainly improved the understanding of the benefits

of an individual ability, the use of spatial memory, on the foraging efficiency of herbivores [18]. Yet these simulated herbivores foraged within a group. In the model, the behaviour of each sheep was determined by about forty parameters, nine controlling its movements (direction and speed), six its spatial memory, and another three the way an individual is attracted by its peers [18]. We simulated the way groups of three sheep searched for a preferred food (i.e., bowls containing pellets) hidden in an aggregated pattern within a grass plot, and used experimental data [19] to calibrate the model parameters. We then used the model to assess how the efficiency of this searching behaviour was affected by changes in some animal (sociability, memory capacity) or environmental (plot size) factors, and by a combination of these. This showed that conspecific attraction can have disruptive effects on the foraging of herbivores in habitats where patches deplete rapidly, and also that there is an upper limit to the benefits of using spatial memory at pasture [18].

An ABM is also perfectly adapted to integrate the experimentally-demonstrated laws, processes and theoretical frameworks developed in herbivore foraging behaviour. In a recent model, we aimed to describe in a realistic manner the way a herd of ruminants graze a heterogeneous pasture [5]. Proximate choices of an animal were determined by cell distance and direction (defoliation probability is higher for cells in front of the animal), together with the perception of cell quality by the animal [5], and we used experimental data (e.g., [41]) to calibrate these parameters. Social attraction was considered as an animal checked distance from its peers at regular intervals, walking in priority towards the core group when over a parametrised distance from it. As proposed by Bailey et al. [3], the memory of site value decays with time to the average value of sites exploited during the last grazing episodes. We will now use this model to assess the effects of different selection rules (random, matching, optimal choice) and of social characteristics, such as leadership or

social cohesion, on the way a group of ruminants makes use of a grassland and creates heterogeneity. In addition to their ability to model intra-species relationships, ABMs also have proven adequate to simulate inter-species interactions. This approach was implemented within an extensively used mountain area, where horses and cattle were equipped with GPS collars to track their movements and with Ethosys devices to record their activity [29]. Spectral analysis was also achieved on real traces to guess the spatial positions and distribution of the animals.

The possibility to hybridise ABMs with other modelling approaches can further help to deal with the complexity of foraging systems. Though not developed on grazing herbivores yet, hybrid models have already been used to simulate group foraging in other animal taxa. A hybrid model has been explored in Toquenaga et al. [44] where colonial formation and group foraging of birds in a patchy environment are simulated with an artificial life model using a genetic algorithm and a neural network. Another combination has been tested in a spatially explicit model of fish predation combining MAS with fuzzy logic [10]. In addition, a visual simulation enabled the user to change interactively and dynamically the behaviour of the prey and predator which was based on the pursuit uncertainty, the latter being modelled with fuzzy sets. This model also illustrates another perspective offered by adding visual aspects: realistic animation has been produced using VRML (Virtual Reality Markup Language) and could be interactively simulated and manipulated on the Web. This coupling of ABMs with visual interactive simulation helps experts to participate in the search for acceptable solutions. Indeed, visual simulation benefits from our human ability to understand the spatial behaviour of individual entities by observing their movement traces, and this more easily than by observing curves or a listing of the evolution of raw coordinates for each active entity. However, when models are animated, the speed at which the

events are examined visually is considerably slowed down and the user must be warned that he may unfortunately draw conclusions on the basis of samples of an insignificant size if he forgets a thorough statistical analysis. Despite such limits and whatever the future techniques, the main benefit of modelling will remain the improvement of the understanding of complex systems.

5. CONCLUSION

In this overview, we show that the multi-agent system paradigm is used at its best if we need to simulate the complexity of animal spatial interactions and social behaviour. To handle such complexity, mathematical models are showing their limits, since the cumulative effect of individual interactions can lead to unexpected effects, generally impossible to formalise analytically. ABMs are therefore particularly suited to simulate the behaviour of groups of herbivores foraging within a heterogeneous environment. So far, these ABMs have been mainly used as a research tool in animal behaviour to reveal the underlying mechanisms of individual decisions. This proved particularly useful to investigate conditions that are not easily amenable to experimentation, such as the effects of differences in memory capacity or in sociability. It could, however, also be used to simulate the effect of different grazing management practices, which would help researchers and different stakeholders to exchange their views on pasture management. For example, Etienne et al. [21] used an ABM to simulate the effect of different management strategies for sheep farms, forest production and natural resources in the Causse Méjan. The model made it possible to visualise the effects of these scenarios on the main productive (sheep grazing days and timber growth) and environmental (occurrence of endangered plant and animal species, landscape quality) outputs on any spatial entity relevant to at least one stakeholder. As the effects of the different scenarios were col-

lectively viewed and confronted, they highlighted the need to compromise, and led to new scenarios based on more collective management of the pine woodland. These collective scenarios were more effective than any of the individual ones, for limiting pine invasion in this rare grassland-dominated ecosystem.

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