Jul 1st, 12:00 AM

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J. A. Beecham

S. P. Oom

C. P. D. Birch

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J.A. Beecham, S.P. Oom and C.P.D. Birch

[a] *Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, United Kingdom*
(j.beecham@macaulay.ac.uk)

Abstract: An agent based system (HOOFS) has been developed in order to examine the interactions between foraging animals and a spatially explicit description of the environment, including vegetation growth processes. HOOFS makes use of the agent-based approach to develop a model of foraging in which animal decision making processes are explicitly modelled. The model has evolved from one where foraging decisions are based on a simple biased random walk model with an information weighting parameter, through one in which animals decide between direct walking towards an object as against continuous foraging, ending with a model where memory is used. The model was used to study utilisation of heather around grass patches in a heather-grass mosaic. Model refinement using remote imaging and animal GPS data together with appropriate statistical methods shows the way forward in making a model formulation suitable for predictive modelling.

Keywords: Herbivore Foraging, Cognitive models, Animal Behaviour, Individual-based model, vegetation.

1. INTRODUCTION

Agent-based approaches and have been predicted to be the way forward for disciplines such as ecological and socio-economic modelling (Judson 1994, Uchmanski & Grimm 1996) The reasons behind these approaches are well rehearsed: Agent-based models are able to represent environmental heterogeneity, biological complexity, emergent properties resulting from rare events and demographic stochasticities (Gross et al. 1992).

However, their take up in applied modelling has generally been confined to the realm of exploratory models (Janssen et al. 2001, Bousquet et al. 2000 see Railsback 2001 for critique). Predictive models such as those used for the recent Foot and Mouth epidemic have avoided explicit modelling of animal movements and infection (Ferguson et al. 2001).

Levins (1966) characterised models in terms of realism, precision and generality. Good agent-based models are intrinsically more realistic than their mean field equivalents and many agent-based models can be general. However we would question whether simple rules (such as the biased random walk model Farnsworth & Beecham 1999) are sufficient to explain many aspects of actual animal behaviour which are required to make accurate predictions about how animals interact with their environment. More thorough analysis of the patterns of animal movements and their interactions with the environment has led us towards cognitive models (models of the animals' decision making processes) which take into account perception, information processing and memory (Bailey 1996, papers in Dukas 1998). When we move from physical to cognitive models, we have moved from highly general models with some realism, through highly realistic models which are still imprecise, to, eventually, precise models which can be used predictively, for specific situations. The challenges involved in this process include modelling, data collection and data analysis. In this paper we will examine how we have developed cognitive models of herbivore foraging and how we intend to meet these challenges in terms of large scale data collection methods and statistical modelling of cognitive foraging mechanisms.

2. HOOFS MODELS

2.1 The Environmental Substrate

All the animal models used in the simulations have a common object-orientated model of the environment. A raster map of the vegetation classification is combined with one or more layers representing state variables for the vegetation components (biomass, age, maximum relative growth rate etc.) and projected onto a hexagonal mesh. Each cell (or patch) of the landscape is an

object with a link to appropriate models of plant growth, and nutritional value for the vegetation. The state variables are used to determine initial biomass and growth rates.

Typically an asymmetrical sigmoid growth function (Birch 1999) is combined with a Holling type II (Spallinger & Hobbs 1992) functional response (a description of how in intake rate of an animal foraging in a location varies with the amount of food there) and an optional sigmoid digestibility function, to give a function for the food value of a given patch at a given time, t.
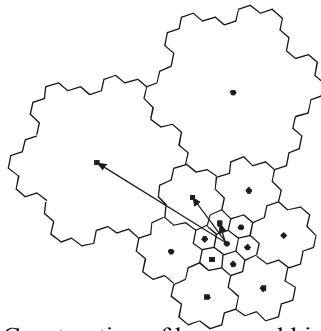

Figure 1: Construction of hexagonal hierarchy and Animal movement evaluation of multiple scales.

For a patch i this quality is designated as $Q_{i,0}$. The patches are arranged in a hexagonal hierarchy as shown in fig 1. Clusters of seven patches are referred to as superpatches of order 1. These superpatches can be further grouped into higher order superpatches. Each superpatch i of order n has an aggregate quality $Q_{i,n}$ which can be obtained by calculating the power law mean:

$$Q_0^\gamma = \frac{\sum_{i=0}^{6} Q_{i,n-1}^\gamma}{7} \ .$$

In fig 2 there is an example landscape made up of 7^5 small patches of two types.

2.2 The biased random walk model with variable discounting

In the original version of the HOOFS (Hierarchical Object Orientated Foraging Simulator) (Beecham & Farnsworth 1998) model animals foraging movements were described in terms of a biased random walk model with two main parameters β and μ. The animal moves between adjacent patches according to the relationship:

$$p_i = \frac{\sum_{j=0}^{N} 7^{\mu j/2} \left(A_j Q_{ij} + \left(1 - A_j\right) Q_{(i+1)j}\right)^\beta}{\sum_{j=0}^{N} 7^{\mu j/2} \sum_{i=1}^{6} \left(A_j Q_{ij} + \left(1 - A_j\right) Q_{(i+1)j}\right)^\beta} \ .$$

The A constants correct for the non-adjacent alignment of alternative layers of the hierarchy. N is the number of levels in the hierarchy. β is the determinism of the patch choice, ranging from 0 for random to infinity for optimal patch choice. μ determines the impact of long range information on patch choice, so that when $\mu = -\infty$ the decision by the animal of where to move is always based on the perceived quality of adjacent patches to 0 where all scales are equally rate. μ is an example of a cognitive parameter. The animal is receiving information about patch quality at a variety of scales and has to combine this information in order to
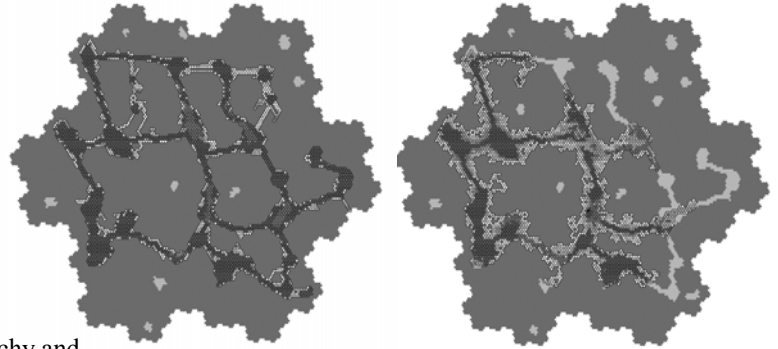

Figure 2: Simulated foraging in grass-heather mosaic a) high β, high μ b) low β, low μ.

make the best decision. The best value of μ will vary with the kind of environment the animal is in and with the amount of competition – short range foraging (i.e. low value of μ) is more profitable when there are lots of competitors. A detailed discussion of these parameters and a sensitivity analysis of their effects on different aspects of grazing is given in Farnsworth & Beecham (1999).

In fig. 2 there are two examples of the model on a simulated mosaic with parameters for the two vegetation types set to those of grass and heather. It can be seen that the animals graze a varying distance into the heather depending, primarily on β. We can estimate β for empirical data on offtake around a grass patch (Hester et al. 1999).

2.3 Walk and Forage action selection model

The diffusional model performed well at explaining foraging within a number of simple landscapes. It did not allow for sufficient speed of movement on landscapes with restricted connectivity, such as when patches of the preferred vegetation are linked by thin paths. In this case the animals are entering a patch primarily to cross it, so food value is irrelevent (Hester et al. 1999).

In our next model animals could choose to foraging or walk. The cost of foraging in a patch is represented by the fixed time of foraging in an empty patch (t_f) plus the time to walk to that patch ($t_{w,n}$), the cost of walking merely by $t_{w,n}$ (n is the number of levels in the hierarchy being traversed). The energetic loss is the time taken multiplied by the maintenance energy, the gain the amount of food obtained times its specific energy. Switching from walking to foraging occurs when:

$$ Q_{i,0} > Q_{i,n} + \frac{t_{w,n}C}{t_f} . $$

The model was modified to deal with the problems of error and expectation. Error is defined as an adjustment to the expected value of the more distant patch, it is represented as a symmetrical uniform deviate of range defined as a fixed proportion of the true value. The expected advantage of moving to a new location will depend upon how many patches will be visited once the move is made. If only a single patch is visited then the travel cost will increase linearly with distance. If the expected number of patches between subsequent moves is proportional to the distance moved then movement cost should be fixed since the cost of moving is divided by a proportional number of patches. A power law expression between the 0th and 1st powers will encompass anything between these extremes. Both the error value and the expectational power law are examples of cognitive model components.

Figure 3: Simulated foraging on digitised landscape with walking and foraging model.

A final enhancement is the decision to follow a line of least resistance even if it is an indirect route. A complex path structure exists on Finella Hill, near Aberdeen, where observations on sheep foraging were made, showing that sheep also have a path following strategy. In the model sheep are allowed to deviate ± 60° from the best direction providing the

travel costs are sufficiently low that $t_{w,n}$ for the indirect route is a specified fraction of that for the direct route (Oom & Hester 1999, fig. 3). Although this model allowed for animal movement across a landscape it was not as accurate at predicting the distribution of heather offtake round grass patches.

2.4 Memory Model

Experience is an adaptive addition to expectation information because it can allow expectation to be updated, and provide a known reference for decision making. Empirical studies support the importance of spatial memory in foraging (Dumont & Petit 1998, Laca 1998). Memory can be categorized in terms of function – spatial memory for location, episodic memory for the sequence of events and associative memory for linking items. Another distinction is between long- and short-term memory. The organisation of memory involves the chunking of memory items (Miller 1956, Healy & Hurly 1998), the relationship between the value of a signal and its persistence (Mackney & Hughes 1995) and effective memory capacity. In addition there is a need for action selection between using memory, using the best perceptual information and adventitious exploration. Our memory model is not a mechanistic model – there are mechanistic models based around neural networks (see Benhamou et al. 1995, Aharonov-Barki et al. 2001), instead it can be characterized as a flexible teleological model. That is to say it is a model designed to achieve a specific functionality, but where that functionality is flexible. Specific features of our model are:

1.) Representation of patches as memory items
2.) Storage of information on location, time and value (Q) of patch (fig. 4)
3.) Selection based on patch quality
4.) Limited capacity modelled by forgetting
5.) Increased capacity for more noteworthy information (i.e. best food sources)
6.) Chunking of smaller memories into larger ones
7.) Limited precision
8.) Decision whether to use memory based on experience versus perception
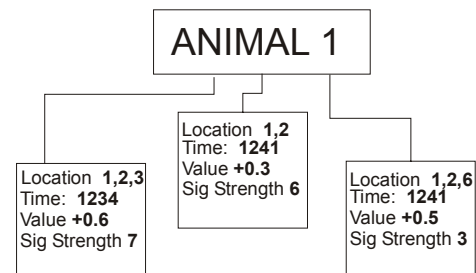

Figure 4: Object structure of memory location information at multiple scales, specified by the different no. of hierarchical coordinates for location.

Animals store locational information using the patch hierarchy. They can store the position of any patch or superpatch. The location of a superpatch is stored hierarchically, as its centre, so that precision is less for higher order superpatches. The signal strength is related to the value being stored (usually increasing with value – remember best, or increasing either side of mean value so that the extremes are more likely to be remembered (Bailey et al. 1996, fig. 5).
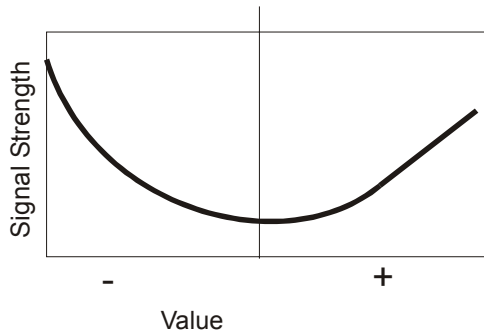

Figure 5: Typical relationship between value to animal of patch visited and strength of memory.

Over time the signal strength decays, unless a patch is revisited, until it falls below a critical threshold and is forgotten. There is a cost per item remembered so that forgetting occurs more often when there is a lot of information to remember.

If a number of patches are stored within a super-patch, the superpatch is stored (and so on up the hierarchy). The chunking behaviour sub-model specifies how any items are needed and how much stronger the composite memory is than the components for each level in the hierarchy.
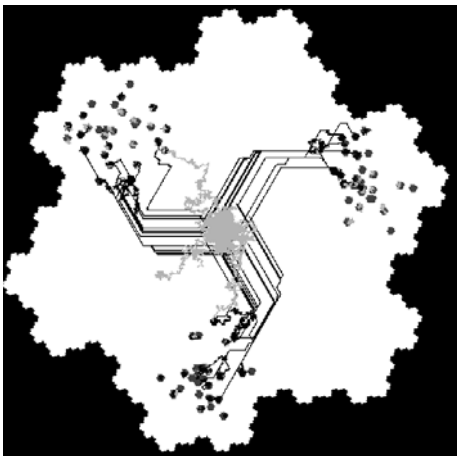

Figure 6: Simulated foraging using memory. The small dark spots are the locations with the highest value. The dark traces represent animals with memory, the lighter ones those without.

The animal selects between the perceived value of Q and the best remembered value. The best remembered value is found by multiplying value by

signal strength. In addition the value may be reduced by a temporal discount to represent the temporary depletion of a resource. In fig. 6 it can be seen that memory results in a more direct movement of animals to the best quality patches. Once this behaviour has been modelled we can compare the effects on intake of memory use. Observations by Dumont and Petit (1998) indicated that a rapid return to high quality patches was observed after repeated learning.

3. MODEL FITTING STRATEGY

Optimisation approaches are amenable to analytical or numerical solution, but because they do not propose explicit mechanisms, they cannot provide a heuristic for explaining departures from the optima. Instead optimisation models have tended to collect a variety of modifications (see Gray 1987 for critique) to make the model fit the observed data. Cognitive models have less well defined optima and because of the limits of cognitive processes are expected to be sub-optimal.

Because of the potentially large solution space of cognitive models, including different uses of memory and variable use of local and global information, a large amount of data is needed to parameterise and validate the very large set of models. Two projects using HOOFS, one in course and one just starting, have attempted to make a comparison between large datasets (one of heather and grass utilisation, the other on animal movements) and foraging models.

3.1 The datasets

Data has been recorded on sheep foraging in a landscape consisting mainly of heather but with areas of grass of varying size connected by a network of paths. A transect survey has been made of heather offtake around grass patches and by image analysis of changes in vegetation. Analyses of the transect have shown that sheep graze heather close to grass patches. The use of heather round a grass patch increases with the size of the patch.

This data has been analysed using a gravity model (i.e. area over the square of the distance) (Oom et al. in press). Previous observations have indicated the tendency for sheep to use path networks (whereas deer are more likely to traverse heather Hester et al. 1999). This sort of information provides constraints for the model parameterisation – how much preference there should be for path movement, selection preference for grass over heather. The simplest form of fitting complex model to complex data is to use judgement to weight these simple

metrics. A less subjective approach would be to make a direct comparison of the predicted offtake with a complete dataset which could be obtained through image analysis of aerial photographs. The disadvantage of this sort of approach is that both the data and the model have substantial stochastic effects between replicates, resulting from arbitrary and unpredictable decisions by the real and virtual animals. Multiple runs of the model with different parameter values help us obtain an estimate of probabilities of one model over another explaining the observations.

The sort of data that has become available recently is that of spatiotemporal information on animal movements obtained from Global Positioning System information. We have used the data of Ian Hulbert at the Scottish Agricultural College (Hulbert & French 2001). As well as GPS time series for individual movements, the vegetation has been classified using the British National Vegetation Classification (Rodwell 1991). In predicting animal movements it is apparent that animals have two decision making criteria – egocentric, based upon the animals' current position, state and direction of movement, and ecocentric – with all decisions being made on the basis of the environment (including other animals). The ideal free distribution (Fretwell & Lucas 1970) model is ecocentric – the animals respond instantaneously and flexibly to obtain the most resources from their environment. Random walk models are egocentric, the position at one moment in time is a probability distribution of distances and times away from a previous position. HOOFS uses both kinds of information and can be adjusted between the two extremes. New work involving modelling telemetry (e.g. GPS) data aims to segregate the ecocentric and egocentric influences on foraging decisions by a range of grazing animals (sheep, red deer, moose) in order to better understand animal decision making.

In both of these projects there is a formidable challenge in fitting complex dynamic models to large datasets. The potentially infinite number of cognitive models that could be fitted to the dataset can be limited by assuming a finite granularity of models and systematising the relationship of the different models to each other. This is already done in a simple way by running the model over a number of parameters in a multi-dimensional rectangular design. HOOFS is a particularly easy system to use in this respect because it is a metamodel. The precise model is specified in a declaration file that can be automatically generated. Two frameworks for choosing between models are a genetic algorithm approach, whereby parameters vary between individuals and are selected according to an optimal or statistical criterion. The second is that of using a Bayesian approach to relative calculate the probabilities of various models, within a specified metamodel context. In analysis of GPS data we can predict the overall distribution of patches visited with a specific model parameterisation and run for a long time to generate a likelihood map and the likelihood of the data fitting this model can be calculated. We can also examine short-term likelihood distributions around a fixed point in time and space which is know to occur both in data and in the model. A GA approach selects animals (from a population with different parameters) and hence models. A Bayesian approach selects between multiple runs and gives an estimate of relative likelihood and so gives more of an overview of the solution but is more cumbersome to operate. The HOOFS framework will allow both model fitting methodologies to be used. Both methods can discriminate between alternative models. Neural Network models are an alternative which has not been followed. Although they can be used to explore a large solution set, their emergent internal mechanics are not always easy to scrutinize, and so are more suited to purely predictive modelling than the largely exploratory models used here.

4. CONCLUSIONS

The barriers to developing agent-based models that are likely to be of interest to resource managers and empirical researchers are formidable. The agent-based approach needs three elements: the models themselves, suitable large datasets and statistical models to relate the two. Recent years have seen advances in all three, partly as the result of advances in computer intensive methods. There is still a lack of synergy between these three advances, probably because all three are cutting edge methodologies and it is easier to deal with problems where at least one of these aspects is straightforward. The HOOFS framework has shown promise as the basis of a more applicable model, but we are still some way off using it predictively.

Stakeholder applications for HOOFS will focus on the spatial information it can generate. As part of a European wide agenda for linking agricultural production with environmental and community aims, the mosaic qualities of landscape are seen as increasingly important. HOOFS can be used to examine the stability of mosaics under grazing and land use scenarios and the implications for biodiversity both of vegetation species and of other animals which share semi-natural environments with productive species.

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