



# Foraging in a complex environment: from foraging strategies to emergent spatial properties

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Received 10 January 2004; received in revised form 13 June 2004; accepted 29 June 2004

Available online 11 September 2004

## Abstract

Spatial interactions between herbivores and vegetation resources drive plant and animal dynamics and ecosystem functioning. Energy maximization is often proposed as an important factor determining diet selection, however, few studies have made the link between different energy-maximizing strategies and emergent properties, such as the spatial pattern of defoliation. Using an individual-based model, we investigate the role of several hypothetical perceptual traits in the formation of defoliation patterns and the consequences for the foraging performance of the animals. Results suggest that in complex mosaics of poor quality vegetation, highly perceptual strategies are not necessarily an advantage, however, perceptual traits can have a strong impact on the spatial pattern of defoliation.

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**Keywords:** Herbivory; Spatial; Vegetation; Emergent property; Individual-based model; Variogram

## 1. Introduction

### 1.1. Emergent properties and individual-based modelling

The hierarchical foraging theory (Senft et al., 1987) predicts that the intensity of plant–herbivore

interactions decrease with increasing spatial scale, as foraging decisions become increasingly biased towards non-foraging tradeoffs (e.g. shelter). At the same time, Illius and Gordon (1993) argue that due to the interaction between feeding allometry and perceptual abilities, herbivores have evolved foraging strategies that simultaneously pursue foraging efficiency and information gathering. As a result of the low contrast in vegetation quality, herbivores are expected to risk small scale inefficiency in order to improve longer term foraging efficiency, thus suggesting that foraging strategies operate at intermediate scales (Illius and Gordon, 1993). Senft et al. (1987) argue that insight into the decision-making

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mechanisms is required to understand herbivore foraging strategies, thus stressing the role of individuals in the formation of foraging patterns. Cognition, i.e. how animals transform information into perception, is expected to play an important role in foraging behaviour (Bell, 1991; Bailey et al., 1996; Illius and Gordon, 1993). Here, we consider how the pre-ingestion information (Illius and Gordon, 1993) used by herbivores to evaluate the availability of forage in their environment affects the pattern of distribution of defoliation across a vegetation mosaic.

The distribution of defoliation by a population of grazing herbivores across a vegetation mosaic can be seen as an emerging property (Kawata and Toquenaga, 1994) resulting from the interactions between vegetation pattern and individual foraging decisions. A large number of local foraging decisions (entities at lower level), made by individuals in a population, can accumulate to an emerging global pattern of defoliation (emergent property). While a population-based model can be used to investigate the best possible distribution of foragers across a vegetation mosaic, an individual-based model is required to ask what defoliation patterns result from specific individual-based foraging strategies (Grunbaum, 1998).

Experimental progress on spatial predator–prey interactions has been slow due to the complexity and resource demands of hypothesis-testing experiments (Dunning et al., 1995; Kareiva, 1989). Therefore, it is recognized that models can facilitate the investigation of hypotheses at a range of spatial and temporal scales (Dunning et al., 1995; Pyke, 1983). Although a large body of work is focussed on models, which assume omniscient consumers with unlimited access to resources (a.o. Lessells, 1995; Krivan, 2003), we have limited our review to models that explicitly model space. Although, a range of models consider spatial aspects of foraging herbivores (e.g. Gross et al., 1995; Gardner et al., 1989; Jeltsch et al., 1997; Hyman et al., 1991; Bernstein et al., 1988; Roese et al., 1991), two explicitly model the role of foraging behaviour and particularly the role of perception in foraging decisions (Moen et al., 1997; Turner et al., 1994). These conceptual models investigate the performance of animals, using alternative foraging strategies in complex heterogeneous landscapes.

The EASE model (Moen et al., 1997) considers the foraging behaviour of moose (*Alces alces*); the model is spatially explicit only at the scale of neighbouring cells. The foraging strategies in EASE are a combination of stopping and movement rules, determining how much animals eat in the current patch and when they leave. For example, with the ‘Fixed stopping rule’ the animals eat 33% of the current browse in the feeding station and then move to a new feeding station. When deciding where to go, the animals only consider their neighbouring feeding stations and thus do not use information about the environment at a larger scale. The model focuses on energy budgets, ignoring the spatial distribution of defoliation. Cognitive foraging strategies, i.e. where movement is biased towards better browse, performed better than non-cognitive foraging strategies. The differences between strategies increased with decreasing browse density, in line with theoretical predictions (e.g. Stephens and Krebs, 1986).

The model by Turner et al. (1994), developed to simulate the grazing system of northern Yellowstone Park, uses multiple-scale foraging rules. Apart from a random, one-step rule, the animals can either select the nearest resource site, or select the best direction of movement based on knowledge of the environment. Animals can move multiple cells in one time step. The search radius of the animal is set to the maximum moving distance per day. Again strategies are most divergent in their effects at low resource density. Variability of forage intake increases with increased resource heterogeneity. Turner et al. (1994) also do not consider the spatial pattern of defoliation resulting from the different foraging strategies.

## 1.2. Observed emergent patterns of defoliation

In this paper, we investigate the spatial plant–herbivore interactions in a grazed moorland ecosystem in the Scottish Highlands, UK. Patchy distributions of animals across these heather (*Calluna vulgaris* (L.) Hull) – grass mosaics were described as early as the 1960s (Hunter, 1962; Job and Taylor, 1978). A series of experiments in the 1990s (Clarke et al., 1995a; Cuartas et al., 2000; Hester et al., 1999) showed that sheep (*Ovis aries*) and red deer (*Cervus elaphus* L.) exhibit a strong preference for grass, resulting in a large proportion of grass in the diet

despite relatively low abundance of grass in the mosaics. Heather defoliation was strongly spatially correlated with the availability of grass, such that the heather defoliation decreased rapidly with distance from the grass-heather edge (Clarke et al., 1995b; Hester and Baillie, 1998) and heather defoliation increased with the total area of grass in the local (25 m) vicinity (Oom et al., 2002). These results show that only a small proportion of the heather in the mosaic is intensively used and that the use concentrates on heather spatially associated with high grass abundance.

### 1.3. Investigating emergent patterns through field and virtual experimentation

A field experiment was carried out, to increase our understanding of emergent patterns of heather defoliation (Oom et al., 2002). Although, the experiment provided quantitative information on the pattern of heather defoliation, it did not provide insight into the role of foraging behaviour in the formation of the pattern of heather defoliation. To address this issue, we have investigated the effect of foraging behaviour, using an individual-based herbivore foraging simulator. A series of virtual experiments considered the effect of different perceptual parameters, which formed the foraging strategies used by herbivores grazing on an artificial vegetation mosaic. The experiments were executed using an extended version of the HOOFS model (Beecham and Farnsworth, 1998). Parameterizations were based on the grazed ecosystem found in the Highlands of Scotland, considering a herbivore, such as sheep or red deer, foraging on heather-grass mosaics.

The model output contains many variables, which could be described as emergent properties, including: energy intake rate of the herbivores, time spent grazing and diet composition. These properties provide insight into the effect of perceptual ability on the foraging success of the animals. However, the emergent properties shared by both the experimental observations and the model simulations, were the spatial pattern and severity of heather defoliation. In order to facilitate comparison between observed and simulated results, these properties were quantified, using the semi-variogram and the frequency distribution of the heather defoliation.

## 2. Methods

### 2.1. The HOOFS model

The HOOFS (Hierarchical Object Oriented Foraging Simulator) model is a spatially explicit, individual-based model. The model used in the study is an extended version of the model used in previous studies (Beecham and Farnsworth, 1998; Beecham et al., 1999; Farnsworth and Beecham, 1999; Beecham and Farnsworth, 1999; Beecham, 2001). Individual herbivores can have different states and different responses to their environment but in contrast to previous studies (Beecham and Farnsworth, 1999, 1998), individuals interact only indirectly through competition for the vegetation. Parameters for the foraging strategies were all part of the foraging sub-model. A detailed description of the extended foraging sub-model is given in Appendix A. The HOOFS model uses a spatial hierarchy based on a hexagonal grid. Each individual cell, the lowest level in the hierarchy, is a member of a super-cell, consisting of the central cell and its six neighbours. In turn, these first-order super-cells are grouped in second-order super-cells and so on (Fig. 1). Several parameters in the foraging sub-model make use of this spatial hierarchy (Tables A.1 and A.2).

The initial biomass (dry matter) in heather cells was considered representative of the total amount of current year's production, but grass was allowed to grow during the simulation. The grass production was determined by the 'Birch equation' (Birch, 1999). The Birch equation does not have an integrated form, therefore, in HOOFS the new biomass is estimated, using the 'mid-point method' (Birch, 1999). Parameter values are given in Table A.1. Foraging by the animals resulted in depletion of the partial biomass during the simulation. Depletion in each cell depends on the balance between growth and offtake rates.

### 2.2. Field experiment

Heather defoliation distributions were observed on six, 1 ha plots during a three-year grazing experiment at the Macaulay Institute Glensnaugh Research Station. The fenced plots enclosed part of the existing vegetation pattern that had resulted from open hill sheep and cattle grazing. These plots were previously used for a series of experiments, using sheep, deer and cattle

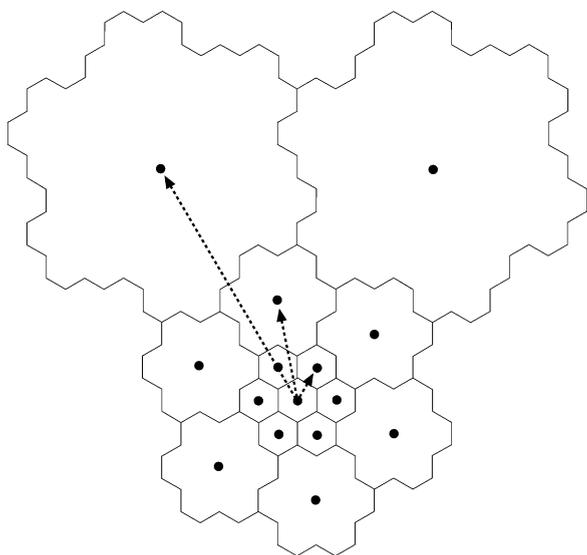


Fig. 1. Arrangement of the first three levels in the hexagonal hierarchy used in HOOFS.

(Hester and Baillie, 1998). Detailed descriptions of the vegetation map and the remote sensing procedures are given by Oom et al. (2002) and Oom (2003). Grazing treatments, with intensities of 4, 3 and 2 sheep  $\text{ha}^{-1}$ , were assigned randomly with two replicates to the six plots. The present paper is based on just one of these plots receiving 2 sheep  $\text{ha}^{-1}$ . Heather defoliation was observed at fixed locations along transects spread across the vegetation mosaics. Transects were perpendicular to the grass-heather edge (Oom et al., 2002).

### 2.3. Vegetation map

The effects of the foraging algorithm in HOOFS (see Appendix A) are dictated by an underlying vegetation map. The spatial patterns of defoliation are the result of the interaction between the specific foraging behaviour characteristics and the characteristics of the vegetation. Although, technically possible, due to computational constraints it was not feasible in this study to vary both the foraging behaviour and the vegetation pattern. Therefore, we have chosen to give priority to the different foraging strategies applied to a single vegetation map.

In order to test the foraging strategies in a realistic vegetation mosaic (Fig. 2), we have used the heather-grass mosaic from a 2 sheep  $\text{ha}^{-1}$  plot of the heather

defoliation experiment (Oom, 2003; Oom et al., 2002). The plot contained a large number of small and medium sized grass patches in a heather matrix, with local clustering of patches and isolated patches elsewhere in the mosaic. Grass patches were connected by an extensive network of paths.

The vegetation map was derived from aerial photographs (Oom et al., 2002). Paths were not detectable from the aerial photographs and were, therefore, surveyed separately in the field and added to the vegetation map. The width of the paths was adjusted to give continuous paths on the hexagonal map of at least one hexagon width. The model used a six level hierarchical hexagonal grid, providing 117,649 cells. The vegetation map was sampled with this hexagonal grid such that each hexagonal cell was allocated the vegetation type present in the centre of the hexagon, while maximizing the number of hexagonal cells occupied by the vegetation map. Due to the rectangular shape of the vegetation map, 65,511 cells were covered by the vegetation map. The remaining cells 'inaccessible' and were not used during the simulations. The resulting hexagonal vegetation map gave a distance of 0.43 m between neighbouring hexagonal cells and a cell area of 0.14  $\text{m}^2$ . The cells in the hexagonal vegetation map (Fig. 2) were 11% grass patches, 5% grass paths and 84% heather.

Initial values of biomass for each vegetation type were based on Birch et al. (2000). In case of heather, only the current year's growth was considered in the model and all current year's growth was available at the start of the simulation. The growth rate of heather was negligible, while grass was allowed to grow during the simulation (Table A.1). Thus, the initial available biomass (g dry matter) of cells was set to 100 g for grass cells (patches and paths) and 500 g (current year's growth) for heather cells (Table 1). As a result 3.5% of the available biomass is grass and 96.5% is heather. The total available dry matter of the whole vegetation mosaic at the start of the simulation was 28.7 tonnes in a vegetation mosaic of one hectare (Table 1). The total production of the vegetation during the simulation depended on the foraging pattern.

### 2.4. Input parameters and output variables

The foraging sub-model is a conceptual model of animal foraging behaviour. Although, it is known that

Table A.1  
Input parameter values used by the HOOFS model

Description	Symbol	Unit	Dim. <sup>a</sup>	Range	Value(s)
<b>Input</b>					
Population size	$N$	–	ani	1–∞	10
Initial energy	$E_{init}$	J	ani	0–∞	5000
Directional persistence (foraging)	$q_f$	–	hier	0–1	1, 1, 0.5, 0.2, 0.5, 1
Directional persistence (walking)	$q_w$	–	hier	0–1	1, 1, 0.2, 0.2, 0.2, 1
Allow turn	$\varepsilon_t$	–	ani	0–∞	1
Mode error	$\varepsilon_w$	–	ani	0–1	0.8–1.2
Determinism	$\beta$	–	ani	0–∞	2
Distance sensitivity	$p_d$	–	hier	0–∞	0.5
Distance exponent	$\mu$	–	ani	0–∞	–0.25
Discriminative ability	$\gamma$	–	ani	0–∞	3, 2, 1, 1, 1
Step cost	$T_{step}$	s	ani	0–∞	0.05
Relative resistance	$R$	–	veg	0–∞	1, 1, 5
Resistance sensitivity	$p_r$	–	ani	0–1	0.02
Inaccessible biomass	$B_{inacc}$	g DM <sup>b</sup>	veg	0–∞	50, 50, 50
Intake rate	$r_{veg}$	g DM s <sup>-1</sup>	veg	0–∞	30, 30, 10
Handling cost	$T_{handling}$	s	veg	0–∞	0.5, 0.5, 0.5
Biomass fraction	$F_{biomass}$	–	veg	0–1	0.3, 0.3, 0.1
Maximum digestibility	$D_{min}$	J g DM <sup>-1</sup>	veg	0–1	0.7, 0.7, 0.5
Minimum digestibility	$D_{max}$	J g DM <sup>-1</sup>	veg	0–1	1.0, 1.0, 0.6
Digestibility recovery delay	$T_{delay}$	s	veg	0–∞	500, 500, 500
Speed of digestibility recovery	$D_{slope}$	s <sup>-1</sup>	veg	0–1	0.001, 0.001, 0.001
Maintenance energy rate	$I_{maint}$	J s <sup>-1</sup>	ani	0–∞	1
<b>Runtime</b>					
Potential energy intake rate	$I$	J s <sup>-1</sup>	cell	0–∞	
Grazing cost	$T_{grazing}$	s	cell	0–∞	
Travel cost	$T_{travel}$	s	cell	0–∞	
Eating cost	$T_{eating}$	s	cell	0–∞	
Biomass eaten	$B_{eaten}$	g DM	cell	0–∞	
Mean resistance	$R_{mean}$	–	ani	0–∞	
Maintenance energy	$E_{maint}$	J	ani	0–∞	
<b>Vegetation parameters</b>					
Maximum above ground SB <sup>c</sup>	$K$	g DM m <sup>-2</sup>	veg	0–∞	150, 120, 525
Maximum growth rate	$a$	g DM m <sup>-2</sup> s <sup>-1</sup>	veg	0–1	0.0013, 0.0001, 0.0001
SB for maximum growth rate	$c$	g DM m <sup>-2</sup>	veg	0–∞	6, 6, 3
<b>Runtime</b>					
Standing biomass	$B$	DM	cell	0–∞	
Time since defoliation	$T_{def}$	s	cell	0–∞	

A set of values is needed when the parameter refers to a level in the hierarchical hexagonal grid or to the three vegetation types.

<sup>a</sup> Dimensions of parameter: hier = six levels of hexagonal hierarchy; veg = number of vegetation types (respectively: grass patch, grass path, heather); ani = number of animal species (one in this case); cell = 117,649 (number of cells in a six level hierarchical hexagonal grid).

<sup>b</sup> DM = Dry matter content.

<sup>c</sup> SB = Standing biomass.

animals have knowledge of their environment and that some of this knowledge is used in foraging decisions, it is unclear how these perceptual processes work (see reviews Bailey et al., 1996; Bell, 1991). The foraging sub-model is thus, an attempt to investigate possible

interactions between perceptual abilities and resource heterogeneity.

To allow the animals to scan and sample the vegetation mosaic efficiently, both a foraging and a walking mode are considered. The foraging mode can

Table A.2  
Output parameters of the HOOFS model. For explanation of dimensions see Table A.1

Description	Unit	Dimension
Animal parameters		
<i>Energy efficiency</i>	%	ani
<i>Energy intake rate</i>	$\text{J s}^{-1}$	ani
<i>Net energy intake rate</i>	$\text{J s}^{-1}$	ani
<i>Movement</i>	step	ani
<i>Grazing time</i>	s	ani
<i>Residence time</i>	s	ani
<i>Biomass intake</i>	$\text{g DM s}^{-1\text{a}}$	ani
<i>Digestibility</i>	$\text{J g}^{-1}$	ani
<i>Heather proportion</i>	%	ani
<i>Grazed area proportion (GAP)</i>	%	veg
<i>Adjusted grazed area proportion</i>	%	veg
Vegetation parameters		
<i>Standing biomass</i>	g DM	cell

<sup>a</sup> DM = Dry matter content.

include movement and subsequent eating, while the walking mode exclusively involves walking. Depending on the foraging strategy and the quality of resources in the vicinity, animals can choose to either walk or forage. A foraging bout is defined as a continuous period spent in foraging mode. These modes are supported by data on rates of movement of sheep in heather-grass mosaics (Hester et al., 1999).

## 2.5. Virtual experiments

To investigate the effects of parameters on model output and interactions between parameters, virtual experiments were executed. The following five parameters from the foraging sub-model were used as treatments in three virtual experiments (Table 3): *determinism*, *distance exponent*, *relative resistance* (Table 4), *discriminative ability* (Table 5) and *distance*

Table 1  
Number of cells and the total biomass in the vegetation mosaic at the start of the simulation

Vegetation	Cells (%)	Biomass	
		%	$10^6$ g DM
Grass patches	11	2.4	0.7
Grass paths	5	1.1	0.3
Heather	84	96.5	27.7
Total	100	100	28.7

*sensitivity* (see Table 2 for a description of these parameters).

Each experiment considered three parameters and each parameter was applied at three levels, leading to a  $3 \times 3$  factorial design. The other parameters of the foraging sub-model were held constant throughout the three experiments and are summarized in Table A.1.

Each combination of parameter values is considered to be a unique foraging strategy. Because, HOOFS is a stochastic model, the replication of runs for each strategy was considered appropriate. Although, the animals started in random locations within the landscape at the start of each replicate run, their movement would be directed to the most attractive parts of the landscape. Thus, replicate runs quickly converged towards a similar foraging pattern. This shows, how strongly the landscape dictates the decisions by the herbivores. As a result, variation in the output variables of replicate runs was low, as indicated by the strong treatment effects and replication was limited to five runs.

The performance of the foraging strategies in the virtual experiments are compared against a non-cognitive strategy with the walking mode switched off (Table 6). A non-cognitive strategy, is achieved by setting the *determinism* to zero, i.e. the animals take random decisions. The walking mode in the model is not directly influenced by the lack of *determinism*. The results for the non-cognitive strategy with walking mode are also given (Table 6). When animals are able to walk as an alternative to foraging, they will walk longer distances and visit more cells. The walking mode is affected by the cost of alternative routes and therefore, leads to a bias towards low resistance. This results in an increased use of paths and patches. Because, walking animals endure travel costs while not taking in biomass, their *net energy intake rate* will be lower compared to the animals that only forage.

## 2.6. Statistical analysis

For each experiment, output variables were averaged across the duration of the simulation run. These average values were then used for analysis in an ANOVA. We deliberately choose the ANOVA, as it is a widely applied statistical tool. Simulations were run for all combinations within a set of parameter values.

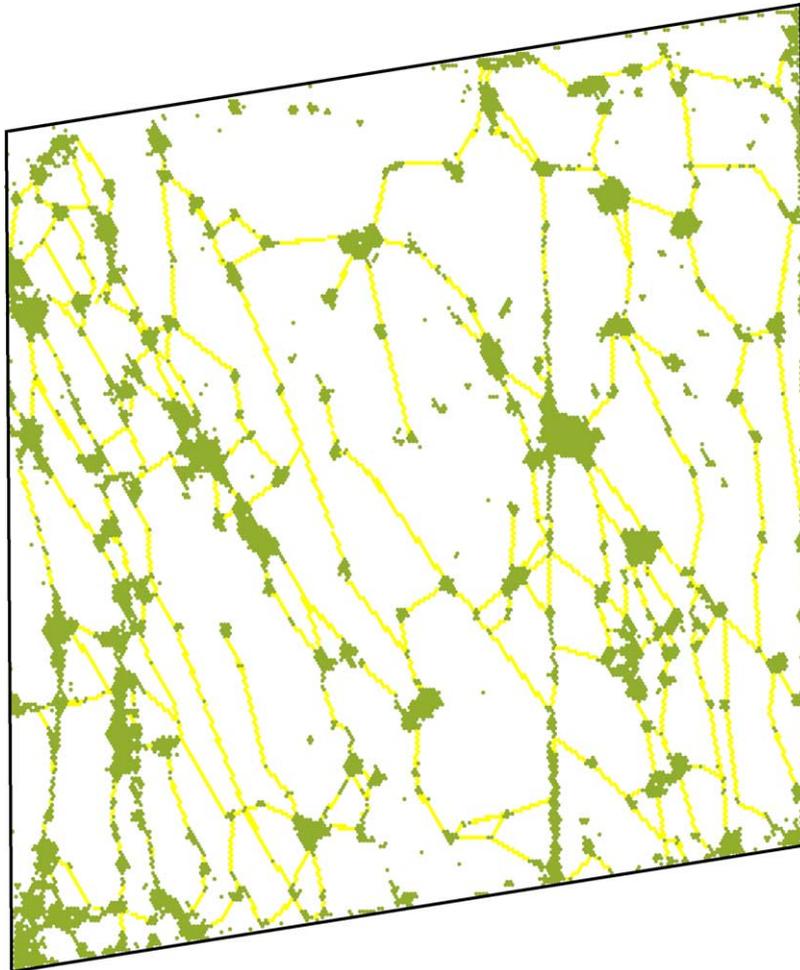


Fig. 2. Vegetation map of the experimental plot on Strathfinella Hill used as the vegetation mosaics in the virtual experiments. The plot is 100 m  $\times$  100 m. Green indicates grass patches and yellow indicates grass paths within a matrix of heather.

The parameter values were considered treatments within the ANOVA, while the output parameters were considered the observations for each combination of treatments. The ANOVA not only provides significance estimates for treatments, but it also provides insights into the interactions between treatments. Generally,  $P$ -values were less than 0.001 and were thus not presented. Several interactions were significant and are mentioned in the text only. The results for the output variables are presented in polar plots. To enable easy interpretation, simulation results are standardized against the results from the non-cognitive strategy without walking mode (Table 6).

The frequency distribution and semi-variogram (hereafter called variogram) were calculated to facilitate the comparison between observed and simulated defoliation patterns. As the simulation model did not include seasonality, observations of cumulative annual grazing were considered most comparable to the simulated defoliation. This was equivalent to the April observations in the field experiment (Oom et al., 2002), covering the whole growing season of heather. Data were averaged by transect (with fixed distances from the grass-heather edge) or location (consisting of an uphill and downhill transect). Only heather defoliation was observed

Table 2  
Description of HOOFS input parameters and output variables

Input parameters	
<i>Determinism</i>	The foraging strategy of the animals is driven by the quality of the vegetation in the vegetation mosaic. How biased animals are towards the best quality vegetation is set by their <i>determinism</i> . When the <i>determinism</i> is zero, the animals forage at random. Animals that are fully deterministic feed only on the best available vegetation and have a <i>determinism</i> of infinity.
<i>Distance exponent</i>	The <i>distance exponent</i> determines what part of the landscape the animals take into account when taking decisions. The <i>distance exponent</i> is similar to the reactive distance as defined by Bell (1991). The <i>distance exponent</i> describes a relationship between the weighting of cell quality versus distance. A <i>distance exponent</i> of zero means that all distances are weighted equal, while a <i>distance exponent</i> between 0 and $-1$ leads to a lower weighting for distant cells, i.e. a bias towards cells nearby. Using an intermediate <i>distance exponent</i> still allows very high quality cells in the distance to influence animal decisions when the cells in their vicinity are of low quality.
<i>Discriminative ability</i>	The decisions of an animal foraging in HOOFS are, among others, affected by the availability of high quality food resources in their environment. The way the animal perceives its environment will strongly influence its decision making. The <i>distance exponent</i> determines how the animal weighs resources near and further away. But when evaluating the food resources, the animal is unlikely to perceive near and distant resources with the same resolution. To accommodate this, HOOFS summarizes the resource environment by calculating mean quality of food resources at each super-cell level of the hexagonal grid. The <i>discriminative ability</i> determines how the mean resource quality is calculated at each level using the individual cells within it. Either the mean is calculated equally across all cells ( <i>discriminative ability</i> = 1), or the mean is biased towards the higher quality cells among the group of cells ( <i>discriminative ability</i> > 1). In ecological terms that means that with a high <i>discriminative ability</i> , animals will perceive small high quality resource cells in the distance even when these cells are surrounded by poor quality cells. The <i>discriminative ability</i> can be set for each level in the hierarchy separately.
<i>Relative resistance</i>	The <i>relative resistance</i> determines the resistance when travelling from one cell to another and affects the <i>step cost</i> . An indication for different perceptions of 'resistance' is shown by Hester et al. (1999) as deer cross grass-heather boundaries more often than do sheep. The resistance encountered when moving from one cell to its neighbour, is calculated as the average <i>relative resistance</i> of the vegetation types in both cells. For example, if the <i>relative resistance</i> of grass and heather are one and five respectively, then going from a grass cell to a heather cell will give a resistance of three. Going from grass to grass or heather to heather will result in a resistance of one and five respectively.
<i>Distance sensitivity</i>	The <i>distance sensitivity</i> determines the willingness of animals to walk long distances when local resources are of low value compared to resources in the distance. A low <i>distance sensitivity</i> facilitates the exploration of isolated patches of high quality resource, while at high <i>distance sensitivity</i> animals tend to forage locally.
Output variables	
<i>Time</i>	HOOFS does not presume any time unit. Instead the time unit is determined by the units used in rate variables, such as the intake rate. Time is expressed as simulation time. All rates are expressed per second, thus simulation time is expressed in the same units.
<i>Standing biomass</i>	The vegetation quantity is expressed as the amount of standing biomass (dry matter) per cell at the end of the simulation.
<i>Energy intake rate</i>	The <i>energy intake rate</i> is expressed as the average <i>energy intake rate</i> in Joule per animal per second.
<i>Net energy intake rate</i>	The <i>net energy intake rate</i> is the difference between the <i>energy intake rate</i> and the energy cost rate endured during foraging, such as movement cost and vegetation resistance.
<i>Energy efficiency</i>	The <i>energy efficiency</i> is the proportion of <i>net energy intake rate</i> in the <i>total energy intake rate</i> .
<i>Movement</i>	The movement is expressed as the average number of steps taken per foraging bout. Moving from one cell to any of its neighbours is considered one step. Continuous grazing in one cell or its neighbour gives a movement of one. Walking several steps before grazing will give a movement value greater than one. As a result of the scaling of the vegetation map, one step is equivalent to 0.43 m in the vegetation mosaic.

Table 2 (Continued)

Output variables	
<i>Residence time</i>	The time animals spend grazing in a particular cell for a single foraging bout, averaged across the landscape.
<i>Grazing time</i>	The <i>grazing time</i> is expressed as the proportion of simulated time spent grazing.
<i>Biomass intake</i>	The average dry matter intake per second across all animals.
<i>Digestibility</i>	The average <i>digestibility</i> of the biomass consumed by all animals during the simulation.
<i>Heather proportion</i>	The diet composition is expressed as the proportion of dry matter of heather in the diet.
<i>GAP<sup>a</sup></i>	The proportion of cells of a vegetation type grazed, calculated for the whole mosaic (total) and for each vegetation type (grass patch, path, heather).
<i>Adjusted GAP</i>	The proportion of cells of a vegetation type grazed relative to the proportion of the vegetation type in the mosaic. For example, the <i>adjusted grazed area proportion</i> for grass is calculated as the proportion of grazed grass cells in the total number of grazed cells in the landscape, divided by the proportion of grass in the mosaic. This gives an indication of the proportion of a vegetation type affected relative to the impact on the whole landscape. When the impact on a vegetation type is close to, or the same as, the impact on the whole landscape, the <i>adjusted grazed area proportion</i> will tend to 100%.

<sup>a</sup> *Grazed area proportion.*

Table 3  
Overview of the three experiments

Parameter	Experiment 1	Experiment 2	Experiment 3
<i>Determinism</i>	[1, 2, 3]	[1, 2, 3]	[1, 2, 3]
<i>Distance exponent</i>	[-0.75, -0.50, -0.25]	[-0.75, -0.50, -0.25]	[-0.75, -0.50, -0.25]
<i>Relative resistance</i>	[Low, Medium, High]	Low	Low
<i>Discriminative ability</i>	Medium	[Low, Medium, High]	Medium
<i>Distance sensitivity</i>	0.5	0.5	[0.3, 0.5, 0.7]

Each experiment applies three values for each of three input parameters, considered within the experiment, in a factorial design with five replicates. See Tables 4 and 5 for explanations of values for *relative resistance* and *discriminative ability*, respectively.

during the field experiment, while both heather and grass defoliation are simulated in the model. To enable quantitative comparison, only the simulated heather defoliation was considered in the statistical analysis.

In order to evaluate the effect of foraging behaviour on the spatial pattern of defoliation, a variogram was chosen because it provides a good method of describing spatial continuity of complex spatial patterns

(Isaaks and Srivastava, 1989). The variogram has its origin in mining, but is slowly being adopted by environmental scientists (Legendre and Fortin, 1989; Legendre and Legendre, 1998; Webster and Oliver, 2001; Goovaerts, 1997; Cressie, 1993).

The model variogram is a function fitted to the sample variogram to provide estimates for the nugget, sill and range (Isaaks and Srivastava, 1989). The

Table 4  
The three parameter values for *relative resistance*, providing a *relative resistance* for each vegetation type

Treatment	Vegetation type		
	Grass	Path	Heather
Low	1	1	1
Medium	1	1	5
High	1	1	10

Table 5  
The three parameter values for *discriminative ability*, providing a *discriminative ability* for each level in the hexagonal hierarchy, where level one is the current cell the animal is in

Treatment	Level in hierarchy				
	2	3	4	5	6
Low	1	1	1	1	1
Medium	3	3	2	1	1
High	5	5	3	2	1

Table 6  
Treatment effects for the two non-cognitive strategies either including both walking and foraging modes, or limited to foraging only

Variable	Foraging only		Walking and foraging	
	Mean	S.D. <sup>a</sup>	Mean	S.D.
Energy efficiency	98.3	0.02	92.6	0.22
Energy intake rate	5.20	0.05	4.93	0.07
Net energy intake rate	5.11	0.05	4.56	0.08
Movement	1.00	0.00	5.34	0.13
Grazing time	91.1	0.1	63.4	0.7
Residence time	3.71	0.06	2.71	0.04
Biomass intake	8.26	0.04	6.64	0.08
Digestibility	62.9	0.32	74.2	0.21
Heather proportion	69.0	2.6	63.4	1.7
Frequency <i>b</i>	0.11	0.01	0.28	0.03
Frequency <i>c</i>	1.99	0.09	2.78	0.25
Range	10.2	4.6	12.7	5.5
Sill ( $\times 10^{-5}$ )	0.73	0.05	0.22	0.03
Partial sill ( $\times 10^{-5}$ )	0.47	0.05	0.10	0.03
Nugget ( $\times 10^{-5}$ )	0.26	0.09	0.13	0.01
RNE	35.1	10.4	58.0	7.7
GAP <sup>b</sup> total	29.2	0.7	35.1	1.4
GAP patch	31.1	3.5	76.8	6.4
Adjusted GAP patch	106.6	11.5	218.6	14.3
GAP Path	31.4	1.7	74.0	3.1
Adjusted GAP Path	107.7	7.6	210.8	2.9
GAP Heather	28.8	0.9	27.7	1.2
Adjusted GAP heather	98.8	1.5	79.0	1.8

The *determinism* is set to zero for both strategies.

<sup>a</sup> Standard deviation.

<sup>b</sup> Grazed area proportion.

sample variogram was calculated and the model variogram was fitted using the GenStat procedures Fvariogram and Mvariogram, respectively (Lawes Agricultural Trust; 5th Edition Release 4.22, Service Pack 2, GenStat Procedure Library Release PL13). The sample variogram for the heather defoliation was calculated using a maximum lag distance of 50 m and a lag size of 5 m. The effect of lag size was tested, but there was no significant effect on the model variogram. Directional sample variograms (Isaaks and Srivastava, 1989) were calculated for 30° sectors centred on the map's east axis: 0°, 30°, 60° and 90°. A single model variogram was then fitted to all four directional sample variograms. Several model variograms were fitted to the sample variograms, but the exponential model variogram (Isaaks and Srivastava, 1989) consistently showed the best fit and is the one used here. This is in line with the suggestion by Webster and Oliver (1990),

that the exponential model variogram is expected to be most appropriate for many ecological processes.

Because, the exponential model variogram approaches the *sill* (general or maximum variance) asymptotically, the *range* (distance at which maximum variance is observed) cannot be determined as the distance at which the sill is reached. For exponential models, GenStat estimates the theoretical range, which is the point at which the variogram reaches 95% of its sill (Webster and Oliver, 2001). The model variogram also provides estimates of the *nugget* (spatially uncorrelated component of the variance plus that which is spatially correlated below the level of the minimum step (lag) size) and the *partial sill* (the spatially correlated component of the variance). The *relative nugget effect* (RNE) (Legendre and Legendre, 1998) was calculated as the contribution (expressed as percentage) of the nugget to the sill, the latter being the sum of the nugget and the partial sill.

The variograms of the simulated heather defoliation are based on average consumption per time step, while observed heather defoliation is based on percentage defoliation per year. Thus, the values of the sill and nugget for simulated and observed heather defoliation are not directly comparable. However, the range is calculated in metres for both the simulated and observed variograms, while the RNE is dimensionless.

In order to compare the frequency distributions of observed and simulated heather defoliation, a probability distribution function was fitted to the frequency histograms of percent heather defoliation. To facilitate curve fitting, only observation with percentage heather defoliation greater than zero were considered. A gamma function generally provided the best fit for both the observed and simulated histograms. The gamma function (Eq. (1)) provides two variables describing the scale (*b*) and the shape (*c*) of the fitted curve (Hastings and Peacock, 1974). The scale variable *b* determines how stretched the distribution is along the *x*-axis. Increasing *b* leads to an increase in the mean and the variance. The shape variable *c* determines the shape of the distribution and effects both the kurtosis (the peakedness of the distribution) and skewness (Hastings and Peacock, 1974; Sokal and Rohlf, 1995). Skewness decreases exponentially and kurtosis decreases linearly with increasing *c*. For *b* = 1 and *c* tending to infinity, the *f(x)* distribution tends to a

standard normal distribution (Hastings and Peacock, 1974). The gamma functions were fitted using the Distribution procedure in GenStat (Lawes Agricultural Trust; 5th Edition Release 4.22, Service Pack 2, GenStat Procedure Library Release PL13). Note that the equation shown here is the one, used by GenStat.

$$f(x) = b^c x^{c-1} \frac{e^{-bx}}{\Gamma(c)} \quad (1)$$

### 3. Results

#### 3.1. General

In order to compare the observed and simulated heather defoliation, two emergent properties were quantified. The first emergent property is the variogram of the spatial pattern of heather defoliation. Fig. 3 shows the sample variogram and the fitted model variogram based on the observed pattern of heather defoliation. The second emergent property is the frequency distribution of the observed heather defoliation. Fig. 4 shows

the frequency distribution of percentage annual defoliation of individual observations.

The individual experiments are covered in separate sections, but some general points are covered here. Differences between output variables for the different treatments and different experiments are small. This is a result of the constraints of the vegetation mosaic. As the availability of high quality grass is limited, the long-term results of different strategies converge. However, instantaneous performance (performance across a small time period) of strategies differ more strongly. Here, we have focussed on the longer-term performance, as we are interested in the resulting cumulative defoliation pattern. In reality, as in the model, animals are strongly limited by the availability of resources. Constraints in the availability of grass and heather in the simulated vegetation mosaic determine the diet composition, with around 60% heather in the diet, despite high *determinism* or perceptual abilities.

The variogram analysis generally shows a large RNE. As stated in the methods, the nugget is assumed to be caused by spatial variation below the smallest spatial scale considered in the analysis, or by a measurement or sampling error (Isaaks and Srivastava,

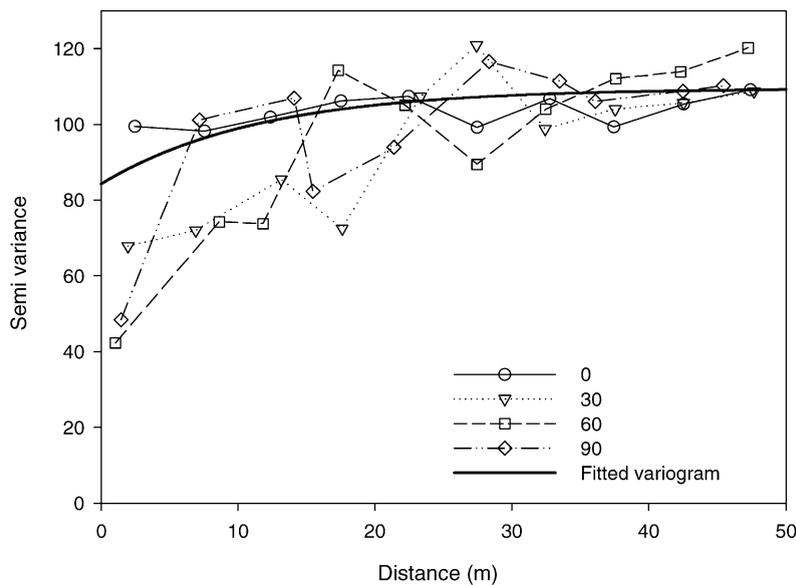


Fig. 3. The sample variogram of the observed heather defoliation pattern based on the 813 locations in the field experiment. Four directional variograms ( $0^\circ$ ,  $30^\circ$ ,  $60^\circ$  and  $90^\circ$ ) were calculated with a lag size of 5 m and a maximum lag distance of 50 m. The model variogram fitted to the four directional variograms, as indicated by the line, is based on an exponential equation resulting in a range of 11.5 m, a nugget of 84 and a sill of 110. The RNE is 77%.

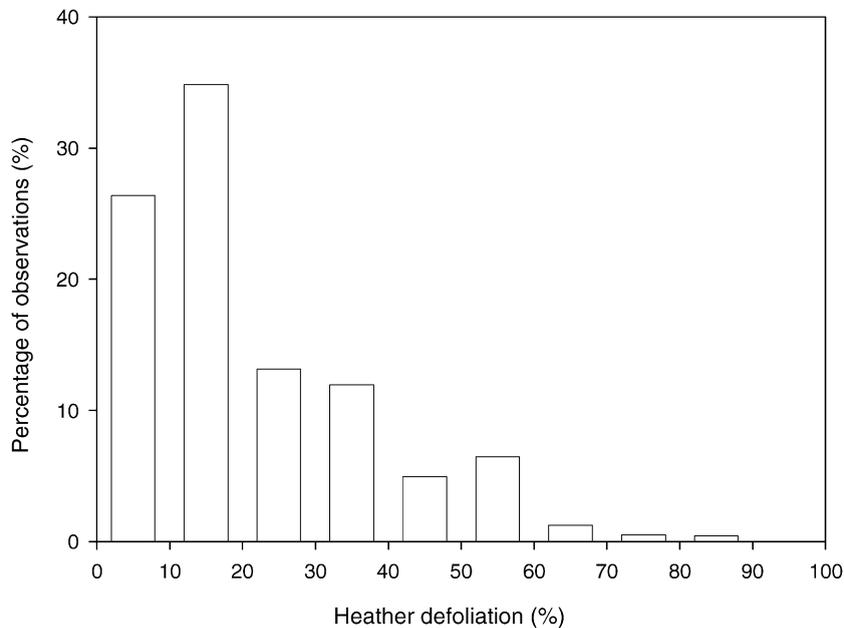


Fig. 4. Frequency distribution of observed heather defoliation for all observations in the field experiment. The frequency distribution variables  $b$  and  $c$  are 0.078 and 1.69, respectively.

1989; Webster and Oliver, 2001). However, this is a virtual experiment, using a computer simulation model, so that measurement error is negligible. At the same time, the spatial pattern of defoliation is not sampled in the experimental sense. The spatial patterns of defoliation based on the hexagonal grid and the sample population are the same. This allowed us to calculate the sample variogram for the smallest possible scale, i.e. that of neighbouring cells. Although, we calculated the variogram with a lag distance of 2.5 m, testing of smaller lag sizes showed no significant effect on the nugget. Possible explanations are mentioned in the discussion.

Sample variograms of simulated heather defoliation showed a hole effect (Isaaks and Srivastava, 1989) in directions running across the hill contours of the experimental site, as the sample variogram decreased at intermediate distance after an initial peak.

This effect is most clear for the  $0^\circ$  variogram, which is perpendicular to the hill contours (Fig. 5), suggesting that the average spacing between paths is around 11 m. Some directional variograms did not reach an asymptote, but increased or decreased with distance (Fig. 5), indicating a non-stationary mean

across scales (Isaaks and Srivastava, 1989), i.e. some areas of the landscape were more heavily grazed than others at the largest measured scale. Implications are described in the discussion.

### 3.2. Non-cognitive strategies

Non-cognitive strategies, or non-cognitive foraging strategies, were simulated as a baseline against which to compare the cognitive foraging strategies. The lack of bias towards higher food quality in this non-cognitive strategy, means the animals eat what they come across, regardless of the vegetation type or quality. In foraging mode only, the animals graze a large part of the mosaic (*grazed area proportions*, GAP), while their *energy intake rate* is low (Table 6). Their movement between foraging bouts is limited to single steps to neighbouring cells, thus *movement* equals one. As movement is limited, both *residence time* and *grazing time* are high. Their diet is of poor quality, but as the animals spend little energy on *movement*, their *energy efficiency* is high. Notable is the large RNE (Table 6). This illustrates that most of the variation in the defoliation is a result of non-spatial

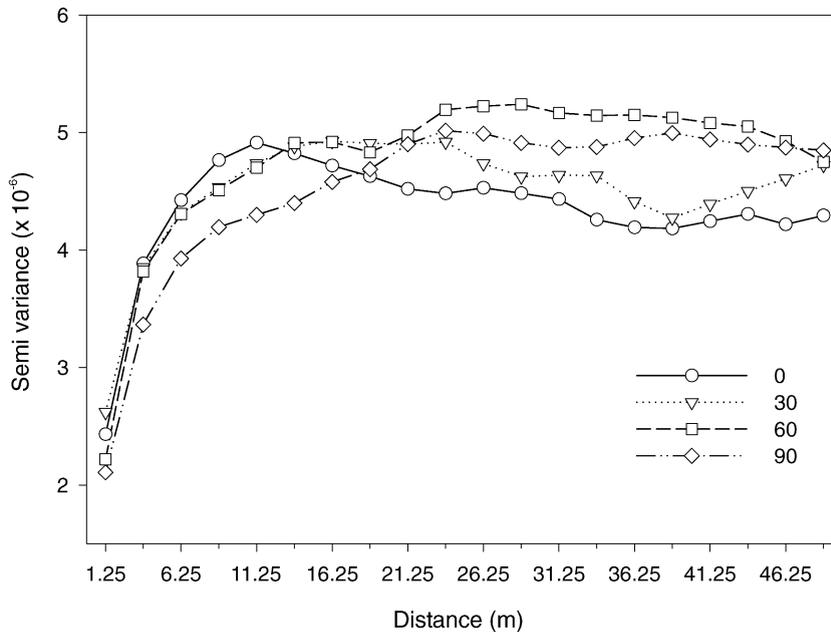


Fig. 5. Example of a sample variogram of a heather defoliation pattern resulting from a model simulation run. The sample variogram was calculated for four directions ( $0^\circ$ ,  $30^\circ$ ,  $60^\circ$  and  $90^\circ$ ) with a lag size of 2.5 m and a maximum lag distance of 50 m.

processes. The remaining correlated variance is a result of the fact that the animals still move from cell to cell.

The diet emerging from the simulations, indicated by the *proportion of heather* in the diet, is determined by the *intake rate* of grass and heather (Table A.1),  $30 \text{ g DM s}^{-1}$  and  $10 \text{ g DM s}^{-1}$ , respectively and the encounter rate of both vegetation types. Therefore, if animals were given equal amounts of grass and heather, the intake rates would result in a diet of 25% heather, but with a heather cover of 90% the ratio of encounter rate of heather to grass is 9:1 (assuming random encounters). This would be expected to give a

diet of 75% heather, however, because the animals start off on the grass (also indicated by the slightly higher *adjusted grazed area proportions* for patches and paths), the *proportion of heather* in the diet is 69% (for the animals with only foraging mode). This discrepancy would decrease with increased simulation time. When animals have the choice of the foraging or walking mode, the animals are still biased (due to the *relative resistance*) to walk on the grass even if their foraging mode is non-cognitive. This decreases the *proportion of heather* in the diet to 63% (Table 6) and shifts consumption to the grass patches and grass paths (Table 7).

Table 7

Biomass (%), per vegetation type, available in vegetation mosaic at the start of the simulation and biomass consumed per vegetation resulting from the non-cognitive foraging strategies

Vegetation	Biomass at start (%)	Biomass consumed (%)	
		Foraging only	Walking and foraging
Grass patches	2.4	22.5	92.8
Grass paths	1.1	10.9	27.3
Heather	96.5	8.3	4.6
Total	100	8.6	6.9

When the walking mode is added to the non-cognitive foraging mode, the animals perform significantly less well. Their *energy intake rate* drops by 5%, mostly as a result of a sharp decline in *biomass intake* (20%). The animals manage to partly compensate by increasing the *digestibility* of the diet (18%). This is because the walking mode is always biased towards grass, leading to an increase in the proportion of grass cells grazed (*adjusted GAP patch* and *path*) and the subsequent grass in the diet (*heather proportion*).

### 3.3. Alternative strategies

The effect of alternative foraging strategies were investigated for the following variables: *determinism*, *distance exponent*, *relative resistance*, *discriminative ability* and *distance sensitivity*.

### 3.4. Determinism

Increased *determinism* leads to an increase in the *energy intake rate* and a decrease in the distance travelled during a walking bouts (*movement*) (Fig. 6). At the highest *determinism*, the animals perform 11% better (*net energy intake rate*) than the animals using a non-cognitive strategy. The *determinism* reflects how flexible animals are when selecting their food. Highly deterministic animals will only eat from the best quality food resource, in this case the grass and their grazing pattern thus becomes limited to areas with lots of grass. This is reflected in the increasing proportions of patch and paths cells grazed (*adjusted GAP patch* and *path*), indicating more intensive grazing on a smaller area of the mosaic. Despite the more intense grazing of grass areas, the pattern of heather defoliation changes little.

Increased *determinism* leads to an increase in both the *frequency variables* *b* and *c*. An increase of *b* indicates an increase in the mean and variance of heather defoliation, i.e. the frequency of high heather defoliation increases, while, both skewness and kurtosis decrease (Fig. 6). In other words, large values of heather defoliation increase in frequency with increased *determinism*. This is caused by the sharper decrease in grazed heather cells (*adjusted GAP heather*), as compared to the *heather proportion* in the diet (Fig. 6).

### 3.5. Distance exponent

The *distance exponent* has an effect on the mobility at the cost of the intake rates. At low and intermediate *distance exponent*, animals manage to keep *biomass intake* stable, but when the *distance exponent* is highest *biomass intake* decreases (Fig. 7).

A strongly negative *distance exponent*, i.e. more weight given to local cells, leads to a higher proportion of the cells visited in the landscape, coinciding with a higher *biomass intake* and maximum *grazing time*. With a less negative *distance exponent*, the animals walk more and across greater distances, thus leading them away from poor or depleted areas. However, this walking is at the expense of foraging, as indicated by the decrease in *biomass intake* and *energy efficiency*. The intermediate *distance exponent* performs 5% better (*net energy intake rate*) than the non-cognitive foraging strategy (Table 6).

### 3.6. Relative resistance

The animals' foraging success is strongly affected by the *relative resistance* of the vegetation (Fig. 8). At low *relative resistance*, the animals successfully graze a large proportion of the grass cells (*Adjusted GAP patch* and *path*) (Fig. 9(a)). Increased *relative resistance* makes walking through the mosaic (largely dominated by heather) too costly. Animals, therefore, refrain from walking long distances and spend more time grazing. Despite this, foraging costs go up and *energy efficiency* goes down (Fig. 8). As animals are forced to overexploit their local environment, leading to decreased *digestibility*, heather defoliation is spread more widely leading to an increase in the *range* (Fig. 9(b)). Animals perform 21% better than the non-cognitive strategy at low *relative resistance*, but perform 11% worse at the highest *relative resistance* of vegetation.

### 3.7. Relative resistance–distance exponent interaction

An interaction (not presented here) occurred between the *relative resistance* and the *distance exponent*, such that the importance of the *distance exponent* decreases with increased *relative resistance*. This suggests that in a highly resistant landscape, the performances of different strategies converge.

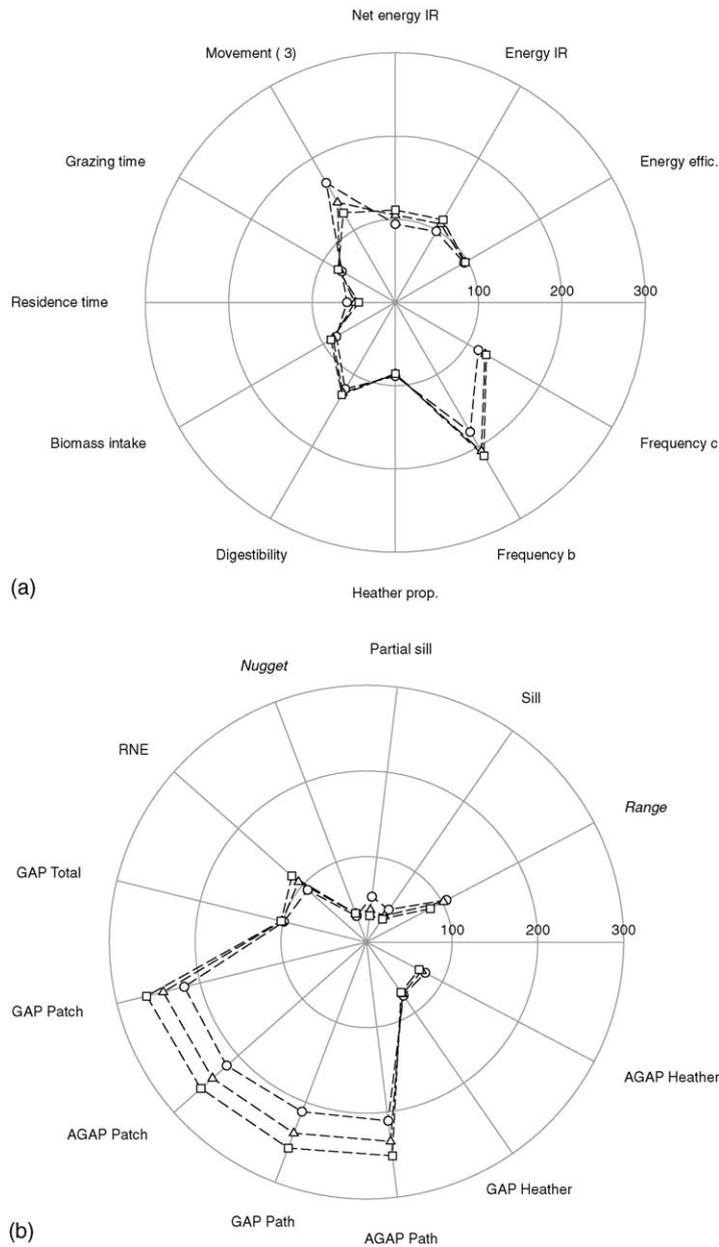


Fig. 6. Polar plot of the output variables for three values of *determinism*, standardized against the non-cognitive foraging strategy using foraging only (Table 6). The three values for *determinism* are: (circles) 1, (squares) 2 and (triangles) 3. Output variables are printed in italic if the effect of *determinism* is not significant.

### 3.8. Discriminative ability

The *discriminative ability* determines whether animals are sensitive to more distant and isolated high quality resource cells. The *discriminative ability*

showed a strong effect on the *range* of the variogram (Fig. 10). A low *discriminative ability* leads to diffuse grazing on only part of the mosaic (Fig. 11 (a)), as animals do not manage to distinguish good from bad. However with improved *discriminative ability*, ani-

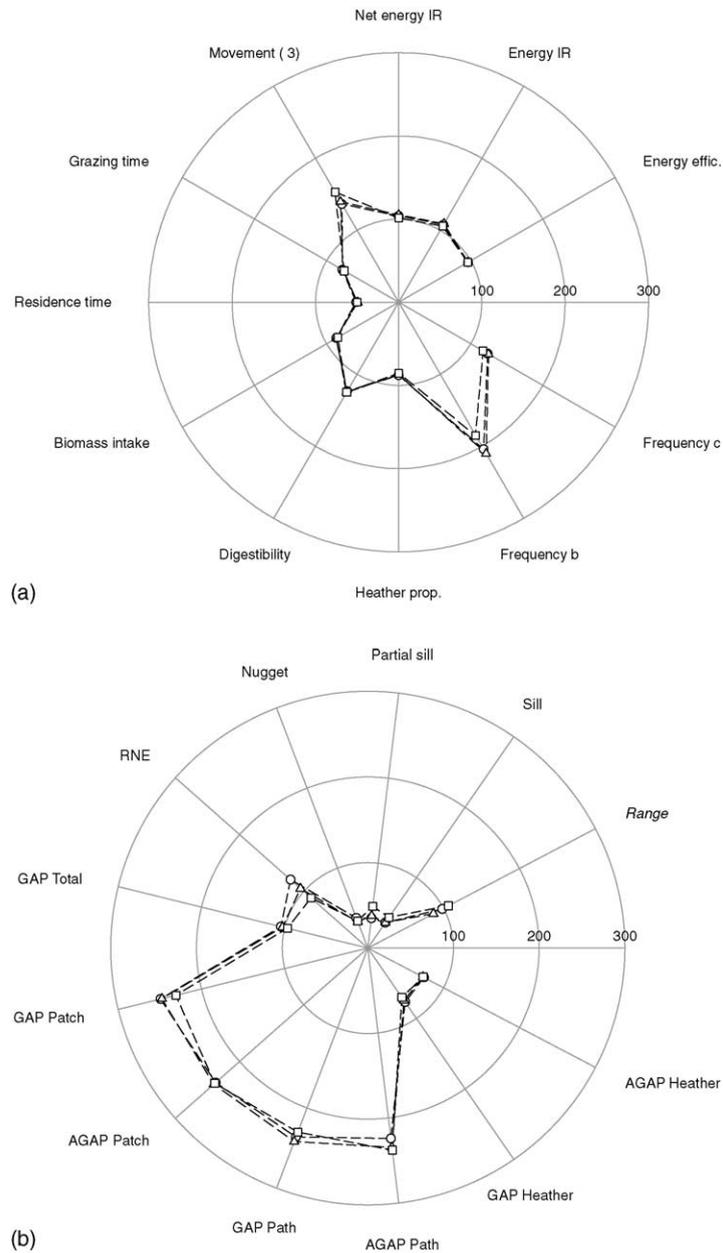


Fig. 7. Polar plot of the output variables for three values of *distance exponent*, standardized against the non-cognitive foraging strategy using foraging only (Table 6). The three values for the *distance exponent* are: (circles)  $-0.75$ , (squares)  $-0.50$  and (triangles)  $-0.25$ . Output variables are printed in *italic* if the effect of the *distance exponent* is not significant.

mals successfully explore the whole complex mosaic, leading to a more spread pattern of grazing highly aggregated on the network of grass patches and paths (Fig. 11(b)). High *discriminative ability* enables the animals to find resource cells more effectively, leading

to a better fit between defoliation and vegetation pattern. The *discriminative ability* also has an impact on the *sill*. As the *range* drops and the defoliation aggregates on the grass network, the spatially correlated variance (the *sill*) decreases. This is the

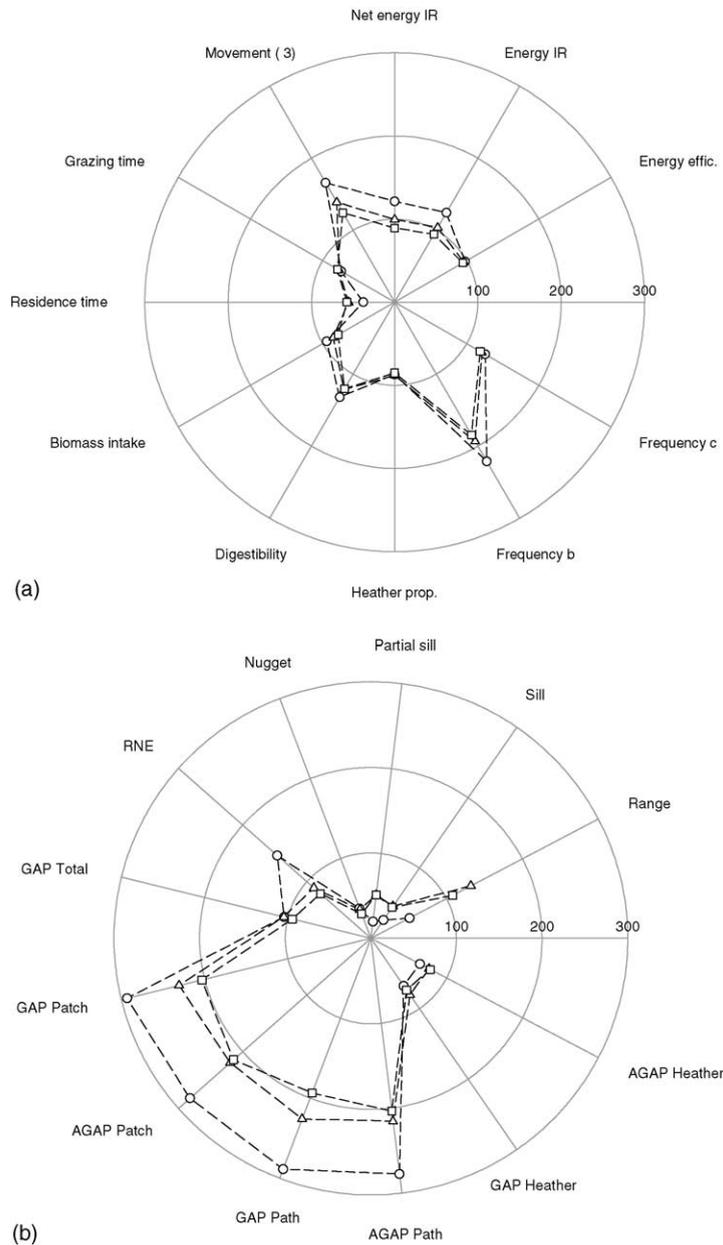


Fig. 8. Polar plot of the output variables for three values of *relative resistance*, standardized against the non-cognitive foraging strategy using foraging only (Table 6). The three values for the *relative resistance* are: (circles) low, (squares) medium and (triangles) high. Output variables are printed in *italic* if the effect of the *relative resistance* is not significant.

result of the increasing use of a small area of the mosaic, leading to a decrease in the small-scale heterogeneity.

Both frequency distribution variables *b* and *c* increase rapidly with increasing *discriminative ability*

(Fig. 10). This coincides with the strong decrease of the *range*. As animals find their way around the mosaic more effectively, their use of the heather becomes more associated with the grass network. The area of heather affected (*grazed area proportion*)

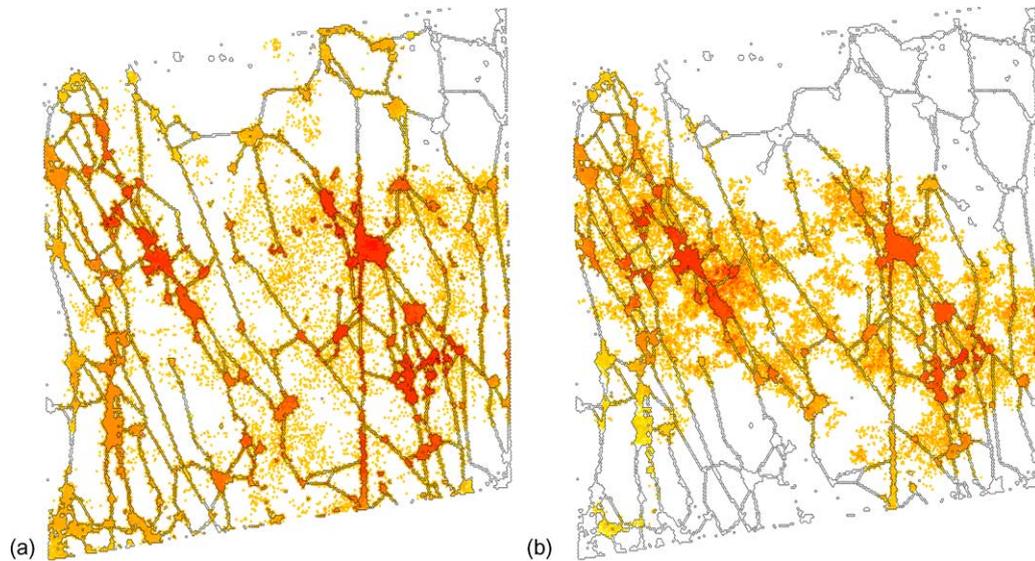


Fig. 9. Defoliation pattern resulting from animals foraging with different degrees of *relative resistance*: (a) low *relative resistance*, (b) high *relative resistance*. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red). The black lines indicate the perimeter of the grass network in the heather matrix. The plot is 100 m × 100 m.

decreases while the severity of defoliation per heather cell increases, leading to an increase in the frequency of high heather defoliation.

Because, high quality resource cells are scattered around the environment, animals have to move further in order to visit these cells (Fig. 10). Although, there is a cost associated with movement, their *net energy intake* remains high at low and intermediate *discriminative ability* due to the increase in *energy intake rate*. The animals can sustain their *energy intake rate* as a result of the higher *digestibility* the animals achieve from the resource cells visited. This coincides with a decrease in *biomass intake*, as the animals spend more time walking. At the highest *discriminative ability*, there is a strongly decreased *grazing time* and increased movement over longer distances. The *biomass intake* thus collapses, resulting in a very poor *energy efficiency*. The animals endure a 7% decrease in *energy intake rate* at the highest *discriminative ability* compared the non-cognitive foraging strategy.

### 3.9. Interaction between *determinism* and *discriminative ability*

The interaction (not presented here) shows that high *discriminative ability* works well with high

*determinism*. The decrease in *energy intake* at the highest *discriminative ability* (as described above), does not occur at high *determinism*, mainly because the *biomass intake* does not decline as strongly (Fig. 10). Instead the animals manage to sustain a 2% increase in *energy intake*.

### 3.10. Distance sensitivity

Increasing *distance sensitivity*, reducing the attraction of remote high quality patches, leads to a strong decrease in the average distance walked and an increase in *grazing* and *residence time* (Fig. 12). While animals manage to explore a large part of the mosaic at the low *distance sensitivity* matching the defoliation pattern to the grass pattern (Fig. 13(a)), the high *distance sensitivity* hampers the perception of quality, leading to a widespread, poorly matched, pattern of grazing (Fig. 13(b)). Increased *distance sensitivity* thus leads to a decrease in the correlation between the grazing and vegetation pattern.

Increasing *distance sensitivity* leads to an increase in the *range* and an increase in the *sill*. As animals increasingly make their decisions dependent on local information, their foraging of the heather becomes less directed and thus more widely spread, leading to

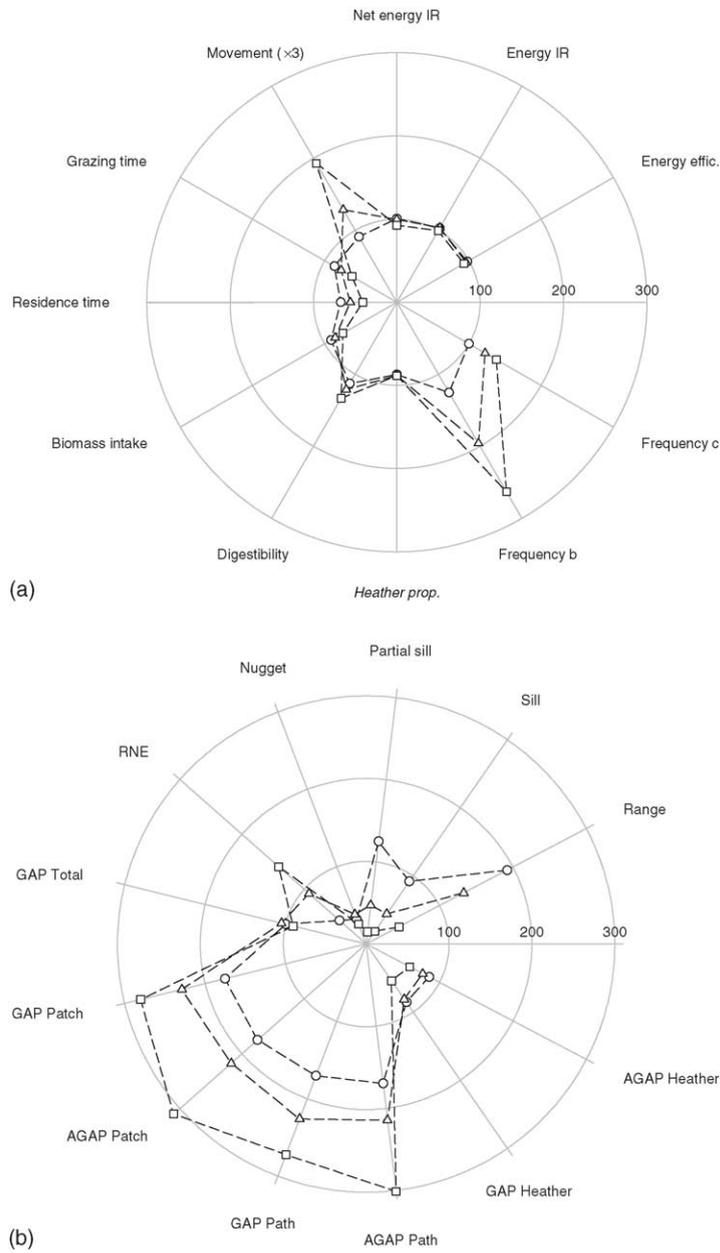


Fig. 10. Polar plot of the output variables for three values of *discriminative ability*, standardized against the non-cognitive foraging strategy using foraging only (Table 6). The three values for the *discriminative ability* are: (circles) low, (squares) medium and (triangles) high. Output variables are printed in *italic* if the effect of the *discriminative ability* is not significant.

increased small scale heterogeneity. Both frequency distribution variables decrease rapidly with increased *distance sensitivity* (Fig. 12). As foraging is increasingly disassociated from the vegetation pattern, more

heather cells are visited with decreasing heather defoliation per cell.

The *heather proportion* is constant for the three values of *distance sensitivity*, despite the strong

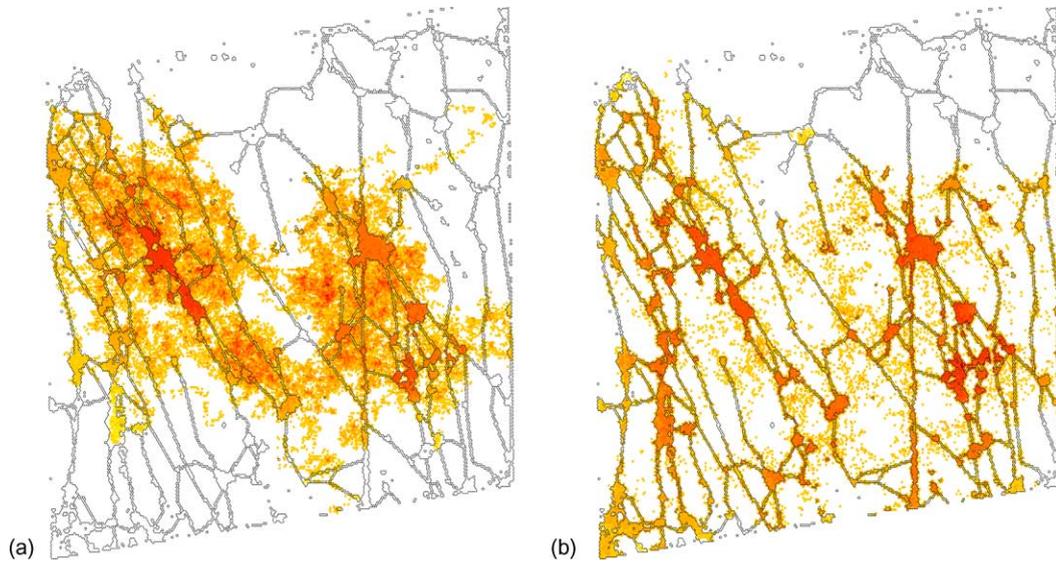


Fig. 11. Defoliation map resulting from animals foraging with different degrees of *discriminative ability*: (a) low *discriminative ability*, (b) high *discriminative ability*. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red). The black lines indicate the perimeter of the grass network in the heather matrix. The plot is 100 m × 100 m.

decrease in *grazed area proportion* of grass patches (Fig. 12). This implies that the grass cells that do get visited will endure a much greater defoliation. As the decrease in *digestibility* is compensated by an increase in *biomass intake*, the *net energy intake rate* remains constant, thus increasing *distance sensitivity* has no effect on performance (*net energy intake rate*) compared to the non-cognitive foraging strategy.

#### 4. Discussion

The results show a strong interaction between the effects of foraging strategies on the performance of the animals and the emergent pattern of vegetation defoliation. Generally, strategies, which led to a large proportion of the mosaic being visited by the animals increased their performance. However, a cost is involved in this exploration and strategies which over-stimulated mobility led to a decrease in *net energy intake rate*. This suggests that high perceptual ability is not necessarily an advantage in complex, generally poor quality, vegetation mosaics.

The pattern of vegetation defoliation was strongly affected by the scale of foraging and the mobility of the animals. An increased scale of foraging, i.e. when

animals have knowledge about more distant cells, led to an increased correlation between the pattern of vegetation and the pattern of defoliation. Although, the overall area grazed remained constant, grazing shifted from a locally dispersed pattern to a globally converged pattern, such that at a large foraging scales, the majority of the defoliation occurred on the grass patches and paths. Higher mobility led to an increase in the small scale, local, heterogeneity. As mobility decreases, grazing becomes increasingly spatially limited, leading to increased pressure on a small area, thus decreasing the variation in defoliation between cells in the grazed area.

Different foraging strategies and resulting defoliation patterns had little influence on the proportion of heather in the diet, suggesting that diet is predominantly determined by the availability and accessibility of the resources. This is in line with observations on the same plots by Cuartas et al. (2000), which show that the proportion of heather in the diet of sheep and deer was affected by the availability of grass, with the proportion of heather increasing with decreasing availability of grass. Additional experiments showed that the proportion of heather in the diet of sheep increased with increasing fragmentation of the grass in the heather matrix, suggesting that the sheep

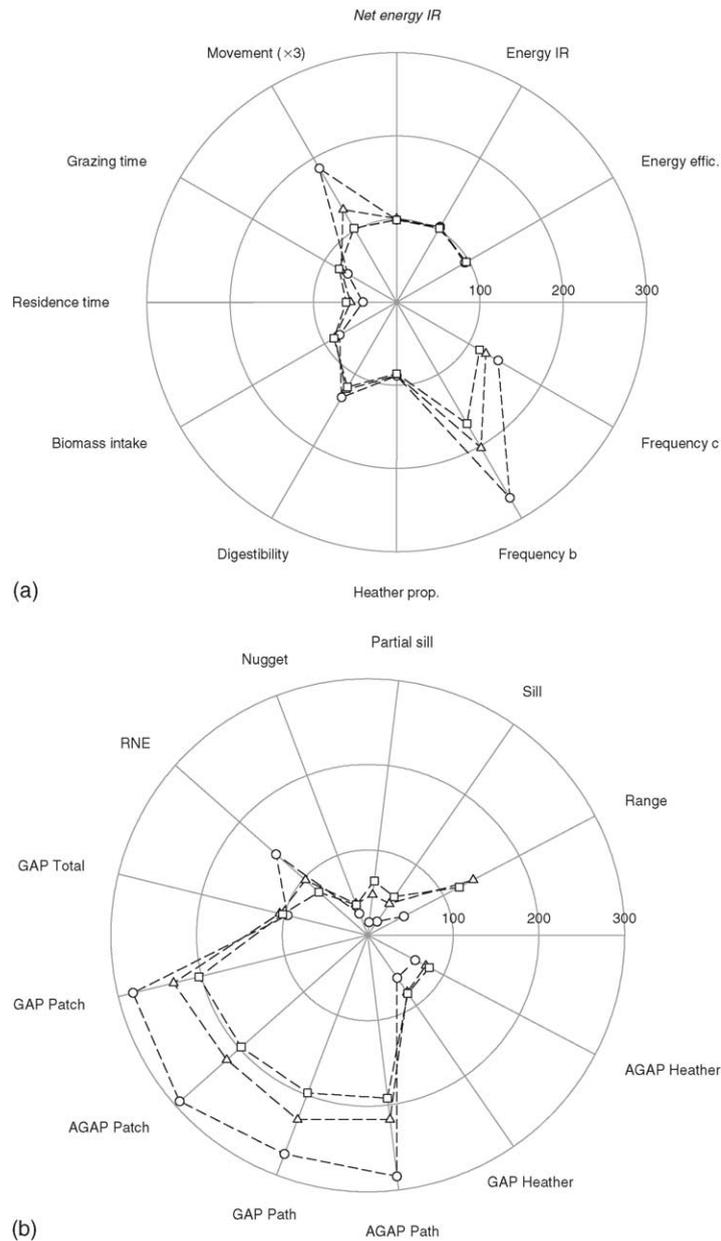


Fig. 12. Polar plot of the output variables for three values of *distance sensitivity*, standardized against the non-cognitive foraging strategy using foraging only (Table 6). The three values for the *distance sensitivity* are: (circle) 0.3, (square) 0.5 and (triangle) 0.7. Output variables are printed in italic if the effect of the *distance sensitivity* is not significant.

became increasingly encounter limited (Cuartas et al., 2000).

One aim of these experiments was to investigate foraging strategies, based on several perceptual parameters that could explain observed defoliation

patterns. The frequency distribution and the *range* of the variogram of the spatial pattern of heather defoliation were used to relate simulated to observed patterns. In a qualitative comparison, the results suggest that a foraging strategy used by a herbivore

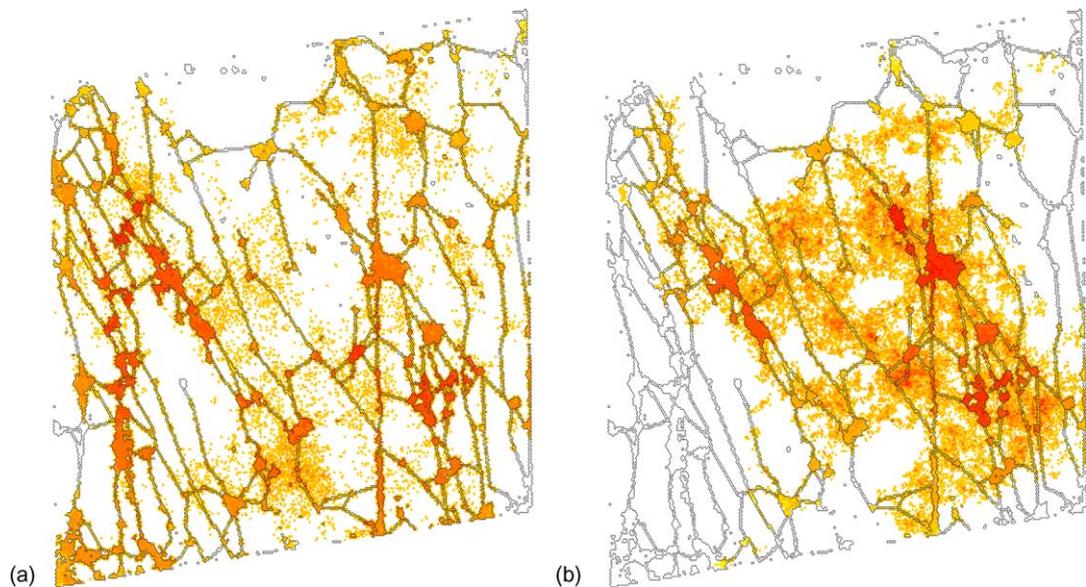


Fig. 13. Defoliation map resulting from animals foraging with different degrees of *distance sensitivity*: (a) low *distance sensitivity* and (b) high *distance sensitivity*. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red). The black lines indicate the perimeter of the grass network in the heather matrix. The plot is 100 m  $\times$  100 m.

would be based on low *determinism*, high *distance exponent*, low *discriminative ability* and high *distance sensitivity*, while the landscape would have high *relative resistance*. This translates as a low perceptual, large scale foraging strategy, facilitated by a network of low resistant vegetation in a highly resistant matrix. However, a quantitative comparison was considered to be inappropriate, as the model was parameterized in order to investigate varying spatial patterns, rather than to be quantitatively realistic. For example, no validation was made to ensure that observed and simulated patterns resulted from the same grazing pressure.

Results suggest that intermediate levels of selectivity and mobility lead to the best animal performance in this artificial environment and result in a strong correlation between the pattern of grass and the pattern of heather defoliation. Furthermore, results show that perception across several scales can contribute to better performance by the animal. This is complementary to the argument of Illius and Gordon (1993), that foraging decisions cannot be made on small scales in time and space. To achieve a high quality diet, animals have to be able to explore their environment. Although, results suggest that highly perceptive

strategies can lead to different diets and patterns of defoliation, differences in performance resulting from these strategies remained small. This indicates that resource heterogeneity, i.e. the complexity of the landscape, has a strong effect on strategy performance. This confirms earlier simulation studies in which performance of strategies converged with decreased abundance of the preferred food resource (Moen et al., 1997; Turner et al., 1994).

Experiments with sheep have shown that the animals can use spatial memory to locate previously visited food patches (Edwards et al., 1996, 1997). It is expected that strategies including some form of spatial memory will do better in heterogeneous/complex mosaics when the strategy allows for a more effective exploration of the mosaic. However, results from this simulation study suggest that the energy return of spatial memory could be limited due to the complexity of the landscape. High perceptual strategies were less successful. Animals could optimize the energy return of spatial memory by varying spatial resolution and extent of the memory. Moderate perceptual strategies might benefit from spatial memory at a low resolution and a large extent. Thus, animals would be more efficient in selecting better quality resource areas at a

larger scale. The implementation of a memory sub model, would provide insight in the role of experience on foraging success in relation to temporal variability of the resource (such as seasonality).

The spatial statistical analysis of the virtual experiments showed three interesting phenomena. Firstly, the model variograms generally showed a large RNE, i.e. a large part of the variation in the vegetation defoliation was not spatially correlated. This also arose from the field observations of heather defoliation, which showed high variation at small spatial scales (Oom et al., 2002). The large RNE could indicate that animals are using strategies similar to biased random walks (Farnsworth and Beecham, 1999; Okubo, 1980) and take random decisions at the smallest spatial scale and biased random decisions at larger scales. On the other hand the effect could be caused by the maximum fraction of available biomass that can be consumed at once in a cell, possibly linked to a fixed amount eaten by herbivores per feeding station (Wallis de Vries et al., 1999). Therefore, further investigation is needed to understand the cause of the large RNE and possible ecological relevance.

Secondly, the sample variograms of the observed heather and simulated heather defoliation pattern, showed a hole effect (Isaaks and Srivastava, 1989), especially for across the hill contours. This hole effect is caused by the directionality and regular spacing of the underlying pattern of paths and patches. The directionality in the vegetation pattern was caused by the interaction between slope of the hill and the defoliation and trampling impact by sheep. As sheep prefer to follow the contours of a hill, paths generally follow the contours (Hester et al., 1999; Oom and Hester, 1999). Thus, the variance between points decreases at the average distance between paths.

Thirdly, the results showed sample variograms which increased up to the maximum lag distance. This suggests that the mean vegetation defoliation of one part of the vegetation mosaic is not equal to the mean at another part of the mosaic. This can be avoided by increasing the size of the simulated landscape (assuming the landscape is homogeneous at larger scales), or by increasing the length of the simulation. The first option would lead to a stabilizing sample variogram at a higher sill and longer range (encompassing the pattern and variance at larger scales),

while the latter would lead to a lower sill and range (a longer simulation period would lead to a more depleted environment with decreased contrast between grazed and ungrazed vegetation). A non-stationary mean suggests that the spatial pattern under study is the result of at least two processes operating at different spatial scales. To ensure a stationary mean, the appropriate scale of observation has to be selected carefully. It is, however, questionable whether complex ecological systems have an ‘appropriate spatial scale’. It is likely that any scale of observation is also affected by processes working either below or above the chosen scale.

In the virtual experiments we have tested the effect of different levels of perceptive ability on foraging performance and, in view of the results, we suggest that high perceptual ability might not be an advantage in complex, generally poor quality, vegetation mosaics. However, through the foraging algorithm we have forced the animals to use a rigid foraging strategy with varying availability of information. It is likely that animals will use different foraging strategies depending on the information available to them and the scale at which the strategy is applied (Illius and Gordon, 1993). Results in this paper show that the cost of lost opportunities increases with distance travelled, reducing the performance of highly cognitive foraging strategies. Therefore, animals are expected to develop cognition primarily for long-range foraging decisions for instance by using spatial memory. This is in line with results presented by Illius and Gordon (1993), which show that sheep use a non-cognitive foraging strategy at a small scale and use collected information about the food resource at larger scales. The use of multiple strategies at different scales needs further investigation.

The biological implications of the presented results concern the evolution of cognition in foraging animals. Although, Hutchinson did not consider cognition when developing the niche concept (Hutchinson, 1959), the results presented here and in Beecham (2001) suggest that cognition could play a role in the formation of ecological niches. Provided that cognition can secure a competitive advantage, animals are expected to develop cognitive strategies, which could lead to a ‘cognitive niche’ (Beecham, 2001). Using the HOOFS model, Beecham (2001) shows that competition can lead to the evolution

of a cognitive niche. The cognitive niche exists when the accessibility of the landscape for the competitor is limited by the accessibility of knowledge about that landscape (Beecham, 2001). This insight in the relationship between heterogeneity and evolution will ultimately bring us closer to understanding the interaction between heterogeneity and biodiversity.

Although, it has been suggested that animals strive towards intake rate maximization (Illius and Gordon, 1993; Newman et al., 1995), it is debatable whether animals pursue optimal foraging (see review Perry and Pianka, 1997). It is more likely that animals develop the skills necessary to survive, improving skills only when pushed by the environment. More generally, in complex adaptive systems it is not global optima that describe the system, instead, through their behaviour, individuals in the system strive to gain an edge over their competitors (Holland, 1992). This study suggests that foraging strategies could play an important part in getting an edge over competitors.

## Acknowledgement

We thank Alessandro Gimona, Iain Gordon and Jon Yearsley for constructive comments and Mark Brewer and Jackie Potts for assistance with the statistical analysis. Sander Oom thanks the Macaulay Development Trust for the funding of his work. Jonathan Beecham and Alison Hester were funded by the Scottish Executive Environment and Rural Affairs Department.

## Appendix A. HOOFS foraging sub-model

The foraging sub-model contains the algorithms concerned with the animals' foraging strategy. The motivation for the strategy is maximization of the quality of the resource cells from which they forage. Every time an animal is ready to forage it will go through a number of decisions. Through these decisions the animal will evaluate its environment, decide the best place to forage and choose how to get there. The decisions are summarized in a flow diagram (Fig. A.1). Although, HOOFS has a social sub-model (Beecham and Farnsworth, 1998; Farnsworth and Beecham, 1999), this was switched off for the purpose

of this study. The model presented here is an extension of the model presented by Farnsworth and Beecham (1999). Input parameters and output variables are summarized in Tables 2, A.1 and A.2.

The measure of vegetation quality is the *potential energy intake rate*, which is determined by the *potential specific net energy* of a cell and the cost endured during a foraging bout. Firstly, the animal gathers the information on the environment for individual cells (Fig. A.1), step (1) and all super-cells (2). Then the animal determines a directional bias (3). After the animal has decided which direction to select, the animal determines the best patch in that direction (4) and determines whether to forage or walk (5) in the direction of that patch. If the animal decides to walk, the animal adjusts the direction in order to take the path of least resistance (6).

### A.1. Update of individual cells

The quality of the environment is measured as the *potential energy intake rate* in each cell or super-cell. The quality of the environment needs to be updated in order to take into account offtake and vegetation regrowth. *Potential energy intake rate* values for a cell are updated after each grazing event or, if the cell remains ungrazed, every 100 time steps. The *potential energy intake rate* is determined by the *digestibility* of the vegetation in a patch and the travel, search and handling costs associated with the patch.

The *digestibility* is expressed as the *potential specific net energy* ( $D$ ; Eq. (A.1)). As herbivores graze down vegetation, the proportion of dead stem increases, leading to a decrease in the *digestibility*. Thus, the *digestibility* decreases when biomass is reduced and recovers with time since defoliation ( $T_{\text{def}}$ ). The recovery curve is sigmoidal set by the speed of recovery ( $D_{\text{slope}}$ ) and the recovery delay ( $T_{\text{delay}}$ ). The *digestibility* varies between the *maximum* ( $D_{\text{max}}$ ) and *minimum digestibility* ( $D_{\text{min}}$ ) for that vegetation type.

$$D = D_{\text{max}} - \left( \frac{D_{\text{max}} - D_{\text{min}}}{1 + e^{-D_{\text{slope}}(T_{\text{def}} - T_{\text{delay}})}} \right) \quad (\text{A.1})$$

To determine the actual intake rate for a foraging bout, the animal evaluates costs incurred during the foraging bout. The costs considered are: *maintenance cost* ( $E_{\text{maint}}$ ), *travel cost* ( $T_{\text{travel}}$ ) and *grazing cost* ( $T_{\text{grazing}}$ ). The *travel cost* and *grazing cost* are

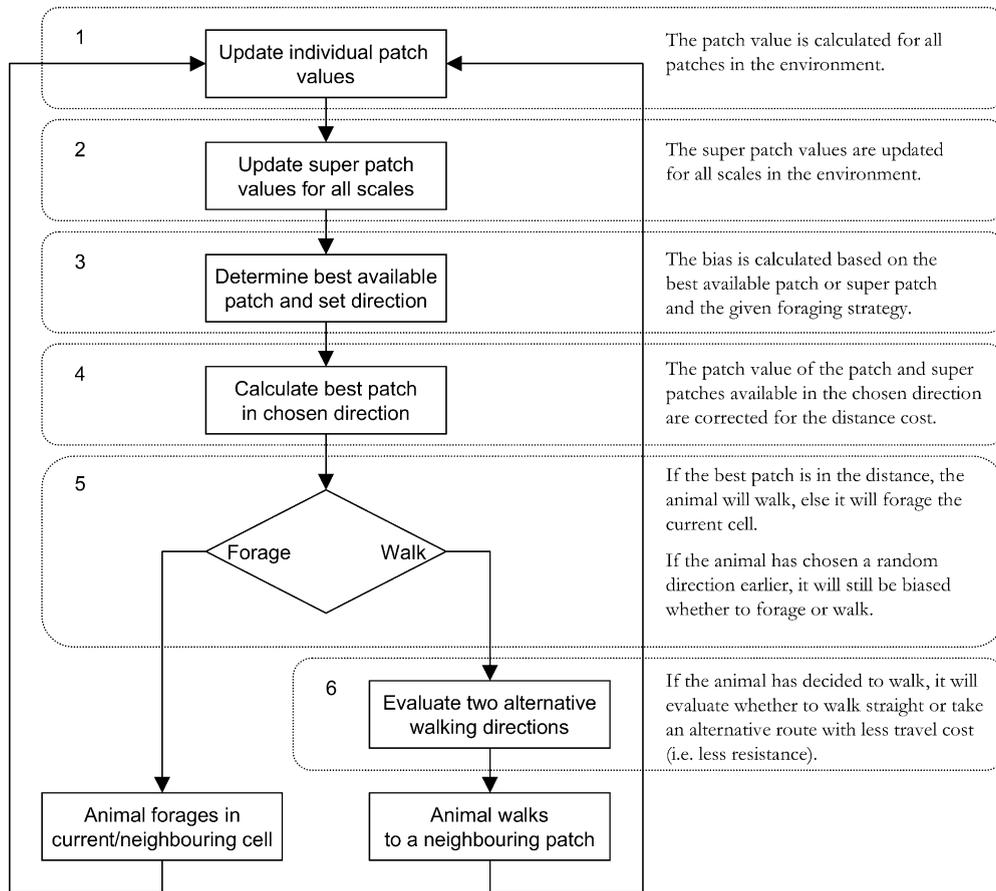


Fig. A.1. Flow diagram of the HOOFS foraging sub-model. Numbers refer to numbers explained in the text.

expressed as time penalties, while the *maintenance cost* is expressed in energy. The *grazing cost* ( $T_{\text{grazing}}$ ; Eq. (A.2)) is the time it takes to consume the biomass, calculated as the *biomass eaten* ( $B_{\text{eaten}}$ ) divided by the *intake rate* ( $r_{\text{veg}}$ ), in addition to a *fixed handling cost* ( $T_{\text{handling}}$ ; putting head down). The *biomass eaten* ( $B_{\text{eaten}}$ ; Eq. (A.3)) is calculated as the difference between the available biomass in the patch ( $B$ ) and the inaccessible biomass (below minimum sward height) for that vegetation type ( $B_{\text{inacc}}$ ), multiplied by the *fraction of the biomass* that can be consumed in one foraging bout ( $F_{\text{biomass}}$ ). Note that the available biomass of heather only comprises the current year's growth. The fraction of biomass available in each foraging bout was introduced to limit the time animals spent in any one cell, in particular in heather cells which have a whole current year's growth as initial

biomass. The *travel cost* (Eq. (A.4)) is the product of the *step cost* ( $T_{\text{step}}$ ) and the *mean relative resistance* ( $R_{\text{mean}}$ ) of the vegetation types travelled through, going from the current cell (a) to one of its neighbours (b),  $R_a$  and  $R_b$ , respectively. The *maintenance cost* ( $E_{\text{maint}}$ ) is the product of the *travel cost* ( $T_{\text{travel}}$ ) and a fixed *maintenance energy rate* ( $I_{\text{maint}}$ ) (Eq. (A.5)).

$$T_{\text{grazing}} = T_{\text{handling}} + \left( \frac{B_{\text{eaten}}}{r_{\text{veg}}} \right) \quad (\text{A.2})$$

$$B_{\text{eaten}} = F_{\text{biomass}} \times (B - B_{\text{inacc}}) \quad (\text{A.3})$$

$$T_{\text{travel}} = T_{\text{step}} + \left( \frac{R_a + R_b}{2} \right) \quad (\text{A.4})$$

$$E_{\text{maint}} = T_{\text{travel}} \times I_{\text{maint}} \quad (\text{A.5})$$

The final *potential energy intake rate* ( $I$ ) is then calculated, using the endured costs and the fraction of the biomass that is indigestible (Eq. (A.6)).

$$I = \frac{(B_{\text{eaten}} \times D) - E_{\text{maint}}}{T_{\text{grazing}} + T_{\text{travel}}} \quad (\text{A.6})$$

### A.2. Update of super-cell values

With the individual cell quality recalculated, the super-cell values can now be updated (Eq. (A.7)) for all higher levels in the hierarchy ( $h+1$ ). The *discriminative ability* factor ( $\gamma$ ) determines how animals perceive aggregation of cells across different levels. A high *discriminative ability* leads to a bias towards higher quality patches within a super-cell.

$$I_{h+1} = \left( \frac{1}{7} \sum_{h=1}^7 I_h^\gamma \right)^{1/\gamma} \quad (\text{A.7})$$

Note that the factor seven in the denominator is replaced by a lower value for incomplete super-cells at the edges of the environment. This is to cope with the square vegetation map in a hexagonal hierarchy. Without the correction, the mean patch value would be higher at the edge of the map, leading to a bias towards the edge. The value is set to induce a slight bias towards the centre of the map.

### A.3. Calculating the foraging bias

Now, the animal is ready to calculate its directional foraging bias, i.e. the bias part of the biased random walk. This is where the animal's foraging strategy is applied to its environment. The animal has six directions to choose from and the directional bias will provide a probability of selecting each direction. A loaded dice will then be thrown taking into account the calculated probabilities ( $p_d$ ; Eq. (A.8)) for each direction ( $d$ ).

$$p_d = \frac{\sum_{h=0}^5 7^{\mu h/2} (A_h I_{dh} + (1 - A_h) I_{(d+1)h})^\beta}{\sum_{h=0}^5 7^{\mu h/2} \sum_{\delta=1}^6 (A_h I_{\delta h} + (1 - A_h) I_{(\delta+1)h})^\beta} \quad (\text{A.8})$$

The foraging bias is calculated using the *potential energy intake rate* ( $I$ ) (Eq. (A.6)) of the neighbouring individual cells and the super-cells at higher scales

(Eq. (A.8)) (Beecham et al., 1999). The bias is influenced by the *determinism* ( $\beta$ ) to select the best possible *potential energy intake rate* and the *distance exponent* ( $\mu$ ). The *distance exponent* determines the weighting of cells near and further away. When *distance exponent* is zero, all distances are rated equal, while a negative *distance exponent* leads to bias towards cells closer by. Although, the bias is calculated in the six directions ( $d$  and  $\delta$ ) of the neighbouring cells, due to the hexagonal hierarchical system, the super-cells are not all aligned with these directions. Therefore, a correction factor ( $A$ ) is applied to the six directions ( $d$  and  $\delta$ ) for the six levels in the hierarchy ( $h$ ). For alternate levels the correction factors are 1 and 0.682, respectively. This is illustrated by the arrows in Fig. 1. Note that a previous implementation of HOOFS used three correction factors based on a different hierarchical ordering of the hexagons (Fig. 1, Farnsworth and Beecham, 1999).

Finally, the *directional probability* ( $p_d$ ) is multiplied with the *directional persistence* ( $q_f$  or  $q_w$ ) (Eq. (A.9)). The *directional persistency* controls the turning behaviour of the animal, making it more or less persistent in maintaining its current direction (compare with turn angle concentration; Bell, 1991). The *directional persistence* is set separately for the walking and foraging mode, to take into account which mode the animal selected previously.

$$p_{d,\text{adjusted}} = p_d \times q_f \text{ OR } p_{d,\text{adjusted}} = p_d \times q_w \quad (\text{A.9})$$

### A.4. Selecting the best patch in chosen direction

When the *potential energy intake rate* ( $I$ ) of the animal's local environment is low compared to its global environment, it is better for the animal to walk instead of graze. The animal can avoid grazing costs in any cells that it walks through. Therefore, the animal should evaluate whether to walk or forage. It also has to decide which patch to select in the chosen direction, which depends on the way it evaluates distance and resistance. The resistance is calculated cascading through the hierarchy (Eq. (A.10)). The resistance at scale  $h+1$  is based on the resistance of cells at level  $h$ , corrected by the *resistance sensitivity* ( $p_r$ ). The *mean resistance* ( $R_{\text{mean}}$ ) is calculated as the average resistance for the total distance travelled. The *resistance sensitivity* determines how animals per-

ceive the resistance across scales.

$$R_{h+1} = \left( \frac{1}{7} \sum_{h=1}^7 R_h^{p_r} \right)^{1/p_r} \quad (\text{A.10})$$

Should the animal evaluate the *step cost* ( $T_{\text{step}}$ ) on the basis of one cell in the distance or should it spread the travel cost across a group of cells in the distance? If the walk results in just a single cell consumed followed by a walk back this would scale with distance. If more cells are eaten with greater distance this scaling is less, i.e. the cost of distance is spread across several cells visited (and thus, less than when only a single cell is visited), down to no scaling (0th power) when the whole super cell is consumed before a further walk of the same or greater magnitude is undertaken. The animal is therefore provided with a *distance sensitivity* ( $p_d$ ). If the power is high the animal thinks that it is worthwhile to walk off into the distance, i.e. it assumes the grass is greener elsewhere.

For all super-cell levels, the value of the *potential energy intake rate* ( $I_{\text{foraging}}$ ) is obtained. This value is corrected with the *walking cost* ( $E_{\text{walking}}$ ) and the fixed *handling time* ( $T_{\text{handling}}$ ) (Eq. (A.11)). The *walking cost* is based on *maintenance energy rate* ( $I_{\text{maint}}$ ), the *step cost* ( $T_{\text{step}}$ ), the *mean resistance* ( $R_{\text{mean}}$ ), the distance between the current animal location and the destination cell ( $Dist$ ) and the *distance sensitivity* ( $p_d$ ) (Eq. (A.12)). Leading to the corrected *potential energy intake rate* ( $I_{Dist}$ ). Note that only a single path, ‘as the crow flies’, is evaluated by the animal. This is not necessarily the path of least resistance.

$$I_{Dist} = I_{\text{foraging}} - \frac{E_{\text{walking}}}{T_{\text{handling}}} \quad (\text{A.11})$$

$$E_{\text{walking}} = I_{\text{maint}} \times T_{\text{step}} \times R_{\text{mean}} \times (Dist^{p_d}) \quad (\text{A.12})$$

#### A.5. Checking for walking or foraging mode

To simulate indecisiveness in the foraging behaviour, the *potential energy intake rate* is then adjusted by the *mode error* ( $\varepsilon_w$ ) (Eq. (A.13)). The *mode error* is taken from a uniform distribution between minimum and maximum *mode error*. A uniform distribution was chosen because this was the least computationally demanding. The animal then evaluates whether to forage or walk depending on the highest value, i.e. if

the neighbouring cell is better than any distant cell it will forage and vice versa. If the animal decides to forage it will now make the necessary steps. If the animal decided a random direction, it will still be biased in the decision to walk or forage. Because, it chose a random direction, it is more likely to walk, as it is likely to be oriented in a less optimal direction.

$$I_{\text{walk}} = I_{Dist} \times \varepsilon_w \quad (\text{A.13})$$

#### A.6. Choosing walking direction

If the animal decides to walk, the walking direction is adjusted to facilitate the animal to follow paths. For the chosen destination cell value, three paths are evaluated. This is done by calculating the two alternative paths relative to the optimal path, taking one initial step to the left or to the right. The destination cell value is calculated as before. The two alternatives are then multiplied by *allow turn* ( $\varepsilon_t$ ) (Eq. (A.14)), thus allowing the animal to either go left or right relative to the optimal direction in order to avoid high travel costs. The animal then chooses the highest of the three values and takes one step in that direction. A possible correction for slope could also be implemented at this stage. This was, however, beyond the scope of this study.

$$I_{\text{path}} = I_{Dist} \times \varepsilon_t \quad (\text{A.14})$$

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