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5 Title: Adaptive Models For Large Herbivore Movements in Heterogeneous Landscapes

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35 **Abstract**

It is usually assumed that landscape heterogeneity influences animal movements, but understanding of such processes is limited. Understanding the effects of landscape heterogeneity on the movements of large herbivores such as North American elk is considered very important for their management. Most simulation studies on movements of large herbivores use
40 predetermined behavioral rules based on empirical observations, or simply on what seems reasonable for animals to do. Here we did not impose movement rules but instead we considered that animals had higher fitness (hence better performance) when they managed to avoid predators, and when they acquired important fat reserves before winter. Individual decision-making was modeled with neural networks that received as input those variables suspected to be
45 important in determining movement efficiency. Energetic gains and losses were tracked based on known physiological characteristics of ruminants. A genetic algorithm was used to improve the overall performance of the decision processes in different landscapes and ultimately to select certain movement behaviors. We found more variability in movement patterns in heterogeneous landscapes. Emergent properties of movement paths were concentration of activities in well-
50 defined areas and an alternation between small, localized movement with larger, exploratory movements. Even though our simulated individuals moved shorter distances than actual elk, we found similarities in several aspects of their movement patterns such as in the distributions of distance moved and turning angles, and a tendency to return to previously visited areas.

55 **Keywords**

Cervus elaphus, neural networks, foraging, ungulate, spatial

Introduction

Movement paths of large herbivores are usually characterized by an alternation between
60 relatively small movements and larger scale excursions (Bailey et al. 1996; Pastor et al. 1997;
Johnson et al. 2002; Frair et al. 2004; Morales et al. 2004). This and other characteristics of
animal movement trajectories should result from the interaction between behavioral decisions
and landscape properties. However, movement behavior in heterogeneous landscapes is still
poorly understood (Lima and Zollner 1996; Zollner and Lima 1999; Morales and Ellner 2002).
65 Here, we use artificial life techniques to explore the connection between the characteristics of
movement paths, animal fitness, and landscape attributes.

Movement decisions should reflect trade-offs between the various factors constraining
fitness. These decisions should vary dynamically as animal activities change both the internal
70 state of individuals, such as hunger and energy reserves (Jung and Koong 1985; Kareiva and
Odell 1987), and the local and global environmental features, such as resources distribution and
abundance (Fryxell et al. 1988; Fryxell 1991; Adler et al. 2001; Fortin 2003), and predation risk
(Lewis and Murray 1993; Schmitz et al. 1997). The interplay between the morphology and
physiology of animals and the characteristics of their food supply impose constraints that may
75 further modulate the movement of foraging individuals. For example, the interaction between
mouth characteristics such as incisor breadth (Illius and Gordon 1987) and plant biomass (plant
size and density) imposes an ‘availability constraint’ to short-term rates of food intake by large
herbivores (Spalinger and Hobbs 1992; Bergman et al. 2000; Fortin et al. 2004), whereas the
interaction between fiber content of plants, gut capacity and food turnover (Illius and Gordon
80 1987) creates a ‘processing constraint’ on long-term rates of energy intake (Belovsky 1984;

Fryxell 1991). Furthermore, internal and external variables influencing foraging decisions by herbivores are likely to change at different rates (e.g. fat reserves accumulation compared to stomach content turnover, or rate of vegetation intake versus rate of vegetation regrowth).

85 The interdependence among internal and external factors, the important number of potentially influential factors, as well as the complex temporal dynamics of these factors makes prescribing behavior for simulation studies, or finding an optimal strategy, quite difficult. Most simulation studies on movements of large herbivores use predetermined behavioral rules based on empirical observations, or simply on what seems reasonable for animals to do (Lima and
90 Zollner 1996), such as choosing to move towards favorable areas. Although important progress has been made by such studies (e.g. Turner et al. 1993; Moen et al. 1997; Farnsworth and Beechman 1999), we believe that additional insights on landscape-animal interactions could be gained using artificial life techniques (Mitchell and Forrest 1995; Huse and Giske 1998; Huse et al. 1999; Strand et al. 2002). We developed spatially explicit individual-based models where
95 behavioral decisions are modeled using feed-forward artificial neural networks (ANNs) whose connection weights are subject to “evolution” through a genetic algorithm (GA). Feed forward ANNs are capable of computing arbitrary nonlinear functions while genetic algorithms can approximate solutions to problems that do not have a precisely-defined solving method (Whitley 2001). Here, we test the general approach in a homogeneous but dynamical landscape and in a
100 patchy landscape with predation risk. As an example, and following a “pattern oriented approach” (Grimm et al. 1996), we run our model on digitalized landscape maps from Alberta and compared daily movement patterns of simulated animals to those observed for eight GPS-collared female elk.

105 We modeled small-scale behavior that resulted in many movement and foraging
decisions during the course of a day. The goal was to determine how such fine-scale decisions
eventually defined broad-scale properties of movement trajectories, and how in turn the
evolution of these properties was influenced by landscape characteristics. In other words, our
focus was not on the fine-scale decisions, but rather on the spatial dynamics of animal
110 distribution that result from these decisions. We concentrated on these properties because this is
the type of information generally available for real animals from tracing studies, and because it is
becoming increasingly clear that the redistribution of individuals is a key process in spatial
ecology (Bolker and Pacala 1997; Tilman and Kareiva 1997; Dieckmann et al. 2000). To fulfill
this objective, we first summarized the simulation outcomes by considering individual locations
115 at the beginning of consecutive days. We then characterized the movement paths in terms of their
turning angles and lengths, and by changes in displacement with time described by redistribution
kernels and squared displacement.

Methods

120 *Model Description*

Simulated animals could adopt two basic movement behaviors: they could choose (1) to forage,
or (2) to explore (*i.e.* move without eating). The outputs of an Artificial Neural Network dictated
which behavior to use, and for how long. When the simulated animal decided to forage, an ANN
was used to determine diet selection, and another one to choose movement direction. Given
125 foraging time and diet preference, the amount of food ingested was governed by a mechanistic
functional response (Appendix 1), and was kept within the limits set by digestive constraints.

Another ANN governed movements when the individual explores instead of eating (Figure 1).

Each day the individuals kept performing different behaviors until they accumulate 13 hours of daily activity, which represents a time constraint that arises from the need to carry out alternative
130 activities other than foraging (Wilmshurst et al. 1995).

The model kept track of energetic gains and losses, and the time spent at different landscape locations. In this implementation we simulated foraging during the spring and summer months, and animals were ranked according to their percent of body fat at the end of the
135 season. Predation risk was represented by a map of risk per unit time, and simulated individuals compounded their experienced risk in proportion to the time spent in each landscape cell. This experienced risk translated into an individual survival probability at the end of a simulation period (150 days). Our measure of “fitness” was the product of fat reserves and survival probability. We took this product of survival and accumulated reserves as our surrogate for
140 individual fitness because fat reserves are critical for winter survival (Turner et al. 1994; Cook et al. 2004), and are related to pregnancy probabilities (Cook et al. 2004). Individuals reproduced in proportion to their fitness and new “character” values were generated according to a fixed “mutation” rate.

145 *Neural Networks and Genetic Algorithm*

All the ANNs used here were feed forward networks (Anderson 1995), with one input layer, a hidden layer and an output layer (Figure 2). Each of the layers consisted of a number of nodes that received data. Different environmental and physiological state variables were used as inputs and there was one node in the input layer for each variable (Figure 1). The input data were

150 multiplied by individual-specific weights that connected nodes between layers. At the nodes of the hidden layer, all incoming stimuli from the input layer nodes were summed and then standardized with a sigmoid function before the signal was sent toward the output node. Similarly, all the stimuli reaching the output nodes were added and standardized (Figure 2). The output values were then translated into a behavioral response by simulated animals. Given a

155 particular combination of input values, the ANN could produce different outputs depending on the values of the connection weights. Thus, the behavior of our simulated animals was governed by the set of weight values used in the ANNs. Several techniques can be used to find the combination of weight values for desired outputs. Most of these techniques require a set of desired “training” outputs, but since we were interested in the cumulative efficiency of

160 behavioral decisions rather than on the immediate outputs of the ANNs, we use a genetic algorithm (Goldberg 1989; Whitley 2001) to search for connection weights that might provide efficient behaviors. All individuals started the simulation with random initial values (uniformly distributed between -5 and 5) for the weight matrices used in the ANNs. At the end of a simulation period (150 days), surviving individuals were ranked according to their measure of

165 fitness (body fat \times survival probability). A new population was then generated with the same number of individuals by creating copies of individuals in proportion to their fitness. There was a fixed probability of 0.02 that a particular value in the set of weights that characterize an individual would change (mutate) by increasing or decreasing its value by an amount drawn from a standard Normal distribution. The weight values were wrapped so that they were always

170 between -5 and 5. This combination of selection and mutation produced populations of increasing average fitness (see results) but there are no guaranties of reaching the global “best” strategy or even staying at that strategy if it is ever reached. Nevertheless, we were able to obtain

a range of “good” solutions to the complex problem of foraging and moving through heterogeneous landscapes.

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Behavioral Decisions

A set of four ANNs was used to govern individual behavior (Figure 1). The “Switch-ANN” decided which behavior the simulated animal should perform, and for how long, by integrating information from eight input nodes. These nodes perceived the state of variables from both the internal and external environment: fraction of gut filled, percent body fat, fraction of daytime already past, Julian date, local food biomass (one node for each of three categories; see *Vegetation Characteristics* below), and local predation risk. Switch-ANN had eight hidden layers and three output nodes. Two of these output nodes were used to choose behavior (Figure 1). The individual followed the behavior corresponding to the output node with greatest output value. In case of a tie, one of the behaviors was chosen at random. If the animal decided to forage, the third output node determined the time, in hours, spent foraging:

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$$t_F = y_T \delta + t_{\min} \quad (1)$$

where y_T is the output value from the ANN (between 0 and 1), δ is a constant (between 0 and 10) also under selection by the GA, and t_{\min} (0.5 h) is minimum foraging time (which could correspond, for example, to a minimum period of resource sampling by foragers).

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The “Diet-Selection-ANN” integrated information on the total amount of forage in the gut, weighted average Neutral Detergent Fiber (NDF) of forage in the gut, and the relative amount of the three categories of plants in the current landscape cell. There were five hidden layers and three output nodes, one for each class of food quality. Output values (range 0-1)

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represented the probability that a given plant category was consumed upon encounter (γ_i in Appendix 1). A scheduler kept track of the duration of the activities performed by each animal and sorted the events to be simulated.

200 Elk position on the landscape was assumed to be in the center of a 28.5-m landscape cell, and movements were among neighboring landscape cells, with the possibility of multiple inter-cell movements within a simulated day. The main differences between a foraging move and an exploratory move were in the type and extent of the information perceived and on the speed of the moves. Our simulated animals were always on the move regardless of whether they choose to
205 forage or to explore. When exploring, the animal always moved at a fixed speed of 4 km/h, whereas the time spent in a landscape cell while foraging was variable (minimum of 30 minutes and maximum of 5 hours), which resulted on varying movement speed. When animals were foraging, the Foraging-Move-ANN decided where to move by processing information on food availability and predation risk in the current and 8 neighboring landscape cells. It also perceived
210 gut fullness as a measure of internal condition. The “Foraging-Move-ANN” had eight output nodes, one for each neighboring cell, and the landscape cell having the highest output value became the next spatial position. In case of a tie, the new position was selected at random among cells with the highest output values.

215 During exploratory movements, individuals had broader spatial perception and perceived variables that changed slower than when performing foraging movements. The “Exploratory-Move-ANN” was sensitive to the internal state of the simulated animal, which was quantified by body fat. We assumed that the individuals knew the date of the season (Julian date) and where

they were in the landscape (given by x and y coordinates). Environmental variables (predation
 220 risks and abundance of the different food types) were assessed at three spatial scales using a
 hierarchical perception framework (modified from Beecham and Farnsworth 1998). The first
 order of perception corresponded to the 8 nearest neighbor cells from which the individual had
 perfect knowledge of their characteristics. The next level of perception corresponded to blocks of
 3 by 3 cells adjacent to the nearest neighbor cells, and a third level of perception corresponded to
 225 blocks of 9 by 9 cells. For these higher order perceptions (levels 2 and 3), individuals perceived
 only averaged values of landscape attributes. As for foraging movements, the Exploratory-Move-
 ANN output was transformed into a movement in one of the 8 possible directions. Some of our
 simulations were conducted on realistic landscapes that included an elevation map. In those
 cases, both the Exploratory-Move-ANN and the Foraging-Move-ANN dictated movement
 230 direction based not only on predation and abundance of the different food types, but also on
 differences in elevation between current position and neighboring landscape cells.

Vegetation Characteristics

We assumed that the landscape was covered with some generic type of grass. The modeling of
 235 plant growth dynamics was based on a modified version of (Turchin and Batzli 2001) regrowth
 model. For simplicity, we considered that each individual plant could take one of three size
 categories (g/plant): $P_{1-3} = [0.5; 3.5; 5.9]$. At the end of a simulated day, a proportion d of
 individuals grew to the next size category, and new vegetation (composed by plants of size P_1)
 was generated at a density-dependent rate of maximum μ_0 . Plant biomass associated with each of
 240 the three plant-size categories (Q_{1-3} in g/m^2) varied from one day (t) to the next ($t+1$) according
 to:

$$\begin{aligned}
Q_1 &= (1-d)Q_1 + \mu_0 \times (1 - (Q_1 + Q_2 + Q_3)/Q_{\max}), \\
Q_2 &= (Q_2 - dQ_2) + dQ_1, \\
Q_3 &= Q_3 + dQ_2
\end{aligned}
\tag{2}$$

where Q_{\max} is the maximum plant biomass (g/m^2) that can occur in a given landscape cell. Plant biomass per category was updated every time there was a foraging event (i.e. reduced by the amount consumed during that event), and regrowth occurred “instantaneously” at the end of a simulated day. Any area would have a mixture of plants of different sizes that would reflect the patterns of vegetation growth and plant consumption by grazers. Animals would have to choose among these food items. As grasses matured, their size increased and their nutritional value decreased (Fryxell 1991). Each plant size (P_{1-3}) was associated with a realistic value of digestibility (in percent): $\text{DIG} = [72; 52; 32]$, and percent of Neutral Detergent Fiber content, $\text{NDF}_{1-3} = [35; 55; 75]$ (Wilmschurst et al. 1995). In each landscape cell, we kept track of the available biomass for each of the three categories of plant.

Biological constraints of modeled individuals

We represented individual body mass (kg) by the state variable W , which was the sum of lean mass (M) and body fat mass (F). Fat mass could be as high as 25-30% of body mass (Moen et al. 1997; Delgiudice et al. 2001). All our simulated individuals were females that started the season with a lean mass of 200 kg and with 20 kg of body fat. Body fat was updated throughout the simulation based on energy expenses and food intake. We used summer estimates of energy requirements from Jiang and Hudson (1992) and Cook (2002) to assume a maintenance cost (E_d) of $445 \times W^{0.75}$ kJ of metabolizable energy per day.

In our model, individuals tried to consume enough food to meet their energetic demands and potential growth. However, the amount of food consumed was kept within the limits imposed by: (1) the time available for foraging, (2) the amount of food that can be ingested during that time given the vegetation available and the forager's functional response, and (3) food processing time. The processing time in the gut increased with the amount of fiber in the diet (Illius and Gordon 1992). We assumed that daily voluntary intake (DVI, in grams) was a good proxy for the maximum amount of food that could be ingested in a day due to digestive constraints. We used the allometric equation reported by (Wilmshurst et al. 2000):

$$\text{DVI} = 2.5 - 0.049 \text{ NDF} + 0.061 W^{0.9} \quad (3)$$

where NDF was the percent neutral detergent fiber of consumed vegetation. The value of NDF used in equation (3) was the weighted average of the NDF of the different food items in the gut of the animals, and the DVI value was updated as the animal ate forage of different qualities.

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Short-term rate of vegetation intake (I , g/min) by herbivores could be controlled either by the rate of food handling in the mouth (cropping and chewing) or by the encounter rate with food items (Spalinger and Hobbs 1992; Farnsworth and Illius 1996; Fortin 2002). We modeled food intake rate based on a mechanistic functional response that accounted for both of these foraging processes (see Appendix 1 for details). This functional response considered that plants of type i of varying quality were accepted in the diet with proportion γ_i (range: 0-1) of their individual encounter rate. The values of γ_i corresponded to the output of the Diet-ANN and could be affected by food availability and internal conditions.

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285 *Seasonal Appetite and potential growth*

(Hudson and White 1985) suggest that the potential growth (PG, in kg/day) and seasonal appetite (CYCL, range: 0-1) of female elk can be estimated based on their body mass and the Julian date (*julday*):

$$\begin{aligned}
 PG &= CYCL \cdot 1.4 + 0.0045 \cdot W \\
 CYCL &= 0.6 + 0.4 \cos(6.186(julday - 182) / 365)
 \end{aligned}
 \tag{4}$$

We used values of *PG* to estimate one of the constraints in food consumption (see below), and to avoid unrealistic growth rates for simulated individuals.

$$PG = \min \left[\frac{CYCL \times 1.4 + 0.0045 \times W}{W_{\max} - W_t} \right]
 \tag{5}$$

Hence, the potential growth rate for a particular day of the year was constrained by appetite and maximum body mass.

Energy Balance

At the end of every simulated day we calculated the energy that each individual spent and gained during the day

$$E_{bal} = E_f - E_d - (E_l \pm E_h)
 \tag{6}$$

where E_f (in kJ) is metabolizable energy obtained from food. The gross energy of grass tissues was set to 18.5 kJ/g while the fraction of grass tissue that could be digested was determined by size-specific digestibility coefficients as described above. We assumed that E_f was 82% of gross energy in digested plant material (Robbins 1993). Daily maintenance cost is E_d (see above) and $(E_l \pm E_h)$ is locomotion cost adjusted by changes in elevation. Locomotion cost of elk scaled with

body mass (in kJ/km) as $12.43 \times W^{0.66}$ (Parker et al. 1984). For simulations that ran in landscapes with topography, the cost of locomotion increased by $20.15 \times \text{slope}$ during uphill movements and decreased by $1.2 \times \text{slope}$ during downhill travels, assuming linear changes with increasing or decreasing slope (Parker et al. 1984). When the energy balance was positive, the excess energy
 310 was fixed as 20% protein and 80% fat (Moen et al. 1997). If the balance was negative, protein and fat were catabolized at the same ratio. The energy content of protein was 22640 kJ/kg, whereas that of fat was 38120 kJ/kg (Robbins 1993).

Landscapes

315 We constructed different landscapes by generating raster maps and controlling the spatial distribution of Q_{\max} (maximum plant biomass). The growth rate of vegetation was set as a fraction of local Q_{\max} and the decay rate was fixed. Performance of simulated animals was evaluated in the following landscapes: (1) homogeneous, (2) patchy with predation risk and (3) actual map of the upper foothills of Alberta, a subset of the rocky mountain foothills studied by
 320 Frair et al. this volume. Their estimates of peak biomass were used to distribute Q_{\max} in a patchy manner that was related to terrain and elevation. A digital elevation model was provided by Alberta Environment (Edmonton, Alberta, Canada). Patchy landscapes were generated by adding 30 bivariate Gaussian distributions with user-defined standard deviation ($\sigma = 30$) and whose centers were at random locations within the landscape. For predation risk, we used a static map
 325 generated by three Gaussian surfaces ($\sigma = 125$) intended to represent predator (e.g., wolf) territories.

All landscape cells represented areas of 28.5×28.5 m. Landscapes were “initiated” by letting vegetation grow for 10 days. After that, 100 individuals were released at random locations within a square of 9×9 km in the center of the landscape. Landscapes included 880×880 cells, which resulted in a density of about 0.16 elk/km². For each landscape, we ran 1000 “generations” of the GA, each consisting of 150 simulated days.

Analysis of Movement Paths

We looked at several properties of movement paths. Daily displacement was measured as the Euclidean distance between the individual’s locations at the beginning of consecutive days. Turning angles were measured as the angular difference between consecutive daily movement directions. Squared displacement (R_n^2) was the squared distance between the starting location of an animal and its location at day n . Mean squared displacement increases linearly with time for simple diffusion, it increases exponentially for movement with directional persistence and it stabilizes for home range behavior (Turchin 1998). To further explore temporal changes in the spatial redistribution of simulated animals we fit Weibull distributions to displacement data (R_n , net distance from release point and location at day n). These distributions can be interpreted as the redistribution kernels for different landscapes. Redistributions kernels are functions that describe the probability that an individual moves a certain distance with time. The Weibull distribution used to fit the displacement data was controlled by a scale parameter (a), and a shape parameter (b). The distribution is quite flexible: It has a fat tail when $b < 1$, it has an exponential tail when $b = 1$, and it has a bell shape, similar to a Gaussian, when b is close to 3.6. Furthermore, under simple diffusion the expected shape parameter value for a Weibull distribution describing displacement is equal to two (Cain 1991; Morales et al. 2004). Thus, the

Weibull not only describes distribution for distance moved under simple diffusion but it also has a very flexible shape, which may approximate distribution of distance moved under other forms of movement (Morales et al. 2004).

355 We compared movement patterns from our simulations in the Rocky Mountain foothills of Alberta with data from elk (8 females) equipped with GPS collars that were relocated daily throughout spring and summer of 2001, which occupied the area within and around our test landscape. Distributions of daily distance moved and turning angles were compared using quantile-quantile plots. If two distributions are the same (or possibly linearly transformed), the
360 points in a quantile-quantile plot should form an approximately straight line. Visual inspection of movement trajectories of both real and simulated animals revealed returns to previously visited areas. We quantified this property by the average number of repeated landscape positions.

Results

365 The genetic algorithm was efficient at improving individual fitness over time. Little improvement in average fitness was observed after 200 generations of simulated elk populations, except for the patchy landscape where fitness increased substantially for about 500 generations (Figure 3). The average fitness in the homogeneous landscape was higher than in the other landscapes because food was abundant and there was no extra cost of predation risk or moving
370 through slopes. We explored differences in behaviors by looking first at properties of daily movements, and then at patterns of redistribution in various landscapes.

The Euclidian distance between locations at the beginning of consecutive days (daily displacement) was, on average, the shortest in the homogeneous landscape (55.3 m, CV 63.71%) and the longest in the patchy landscape (205 m, CV 165.20%). Intermediate values were found on the Alberta landscape (122.75 m, CV 75.33%). Also, daily displacements were much more variable in heterogeneous landscapes than in the homogeneous one. The distributions of daily displacements were all skewed towards short movements, especially for the patchy landscape (Fig 4, A-C). Overall, the angular differences between consecutive daily movement vectors (daily turning angles) revealed many reversals (180° turns) and some directional persistence (0° turns). The distribution of turning angles was more variable in the homogeneous landscapes than in heterogeneous environments, whereas directional persistence was most common in the patchy landscape (Figure 4, D-F).

Mean squared displacement ($\overline{R_n^2}$, squared distance between the starting location of an animal and its location at day n , averaged over all individuals) increased linearly or faster than linearly with time in the homogeneous landscape, whereas it tended to reach a ceiling in other landscapes (dotted lines in Figure 5, A-C). This difference in $\overline{R_n^2}$ between homogeneous and heterogeneous landscapes is especially apparent for the best performing individuals (i.e. those with fitness values in the upper 10% of the fitness distribution). High fitness individuals kept spreading over space in the homogeneous landscape, but quickly stopped getting further from their starting point in heterogeneous landscapes, and concentrated their activities in certain areas (thick lines in Figure 5, A-C). In contrast, poorly performing individuals (lower 10% of the fitness distribution) did not concentrate their activities as much as the best cohorts in the heterogeneous landscapes (Figure 5, A-C). Even though $\overline{R_n^2}$ increased throughout the simulated

time in the homogeneous landscape, it did so at a slow rate due to usually short daily displacements and highly variable turning angles. In contrast, changes in $\overline{R_n^2}$ were more dramatic in the heterogeneous landscapes, which included mixtures of short and long distance moves (see examples of movement paths in Figure 5, D-F).

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Individuals moving in the homogeneous landscape showed a monotonic decrease in the scale parameter of the fitted Weibull distributions (Figure 6, A), meaning increasing displacement distance with time, in agreement with the changes in $\overline{R_n^2}$. In contrast, individuals in heterogeneous landscapes showed an initial sharp decrease in the scale parameter followed by small changes with time, which correspond to fast spread at the beginning of the simulation and little spread later on (Figure 6, B-C). Shape parameters also changed with time. In homogeneous landscapes we found shape parameters close to 1, indicating that the distribution of displacements was close to an exponential (Figure 6, D). Shape parameter for the patchy landscape increased above 2, consistent with a lot of individuals moving similar distances and a tail decreasing faster than an exponential (Figure 6, E). In the upper foothills of Alberta the shape parameter decreased sharply to a value near 1.5, which corresponds to a distribution skewed towards short distance movements but with a few long ones (Figure 6, F).

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Real elk moved much longer distances and showed more extreme values than simulated ones, but the general shape of the distribution was rather similar (Figure 7A). The distribution of turning angles of simulated animals matched quite well that of real elk (Figure 7B). Net displacement was much larger for real elk in Alberta than for our simulated animals, although both showed frequent returns to similar displacement distances (Figure 8). After correcting for

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sampling frequency, simulated animals had on average 34% of their positions in landscape cells
420 already visited, while the average for real elk was only 18%. The highest average of returns was
45.5% for the homogeneous landscape and the lowest (13%) for the heterogeneous landscape
with predation risk.

Discussion

425 All simulated animals based their behavioral decisions on the same physiological constraints
when foraging in various simulated landscapes. Despite such similarities, distinct movement
patterns emerged in different landscapes. An obvious effect of landscape heterogeneity was to
increase variability in movement. In particular, individuals in the homogeneous landscape
consistently moved very short distances. In contrast, individuals in heterogeneous landscapes
430 showed more variable and highly skewed distributions of daily distance moved (Figure 4 A-C).
There was little incentive to move large distances in homogeneous landscapes but it could be
critical to move away from areas characterized by poor food resources and/or high predation risk
in heterogeneous landscapes.

435 In all landscapes, we found a tendency for turning angle distributions to be bimodal, with
animals having an important propensity for 0° (persistence) and 180° (reversals) turns. This
bimodality in turning angles is more evident for simulated elk in heterogeneous landscapes
(Figure 4 D-F), where they either made frequent reversals within “home ranges” or had nearly
straight movement paths when moving away from poor sites or risky areas. Moving in a nearly
440 straight fashion is an efficient search mechanism for finding patchy resources (Zollner and Lima
1999).

Simulated elk showed a strong tendency to confine their movements to relatively well-defined areas within heterogeneous landscapes. At the beginning of a simulation period, our
445 individuals were placed at random locations within the landscape and hence sometimes in areas where there was little or no food, high predation risk, or where steep slopes made moves costly. After a few days some animals found relatively “good” areas in the landscape where they established themselves. Another incentive to stay within a small range was to return to previously grazed areas to consume regrowing vegetation, a foraging strategy previously
450 reported for large herbivores (McNaughton 1984). Interestingly, the highest number of returns was found in the homogeneous landscape, but this was not enough to prevent animals from drifting away from their release point, as evidenced by a steady decline with time in the scale parameter of the Weibull distributions fitted to net displacements (Figure 6) and the temporal increase in mean squared displacement (Figure 5). Net displacement was much larger for real elk
455 in Alberta than for our simulated animals, although both showed frequent returns to previously visited areas (Figure 8).

Our simulated animals moved considerably less than real ones, which might be due in part to an overestimation of food availability in the simulated landscapes. For example, we assumed
460 that simulated herbivores consumed all the above-ground biomass of vegetation, which is generally not the case for actual large herbivores (Hudson and Frank 1987; Fortin et al. 2002). We used a “generic grass” model that could have overestimated vegetation regrowth capacity. For even more realistic models, the generic grass could be replaced with data driven models for vegetation distribution and dynamics, which might include variability due to weather patterns.

465 Furthermore, our models do not include a number of forces that are likely to affect movement
decisions such as social behavior and mating systems. A rudimentary form of spatial cognition
was included in our model as individuals perceived spatial coordinates while performing
exploratory movements. This allowed for simple spatial “memory” to develop through
generations of the GA but better representations of spatial memory could be implemented within
470 the ANN-GA approach. Finally, predation risk was modeled in a static manner but predators
could adapt their home ranges towards areas where prey are more abundant, creating further
incentives for the prey to move (Mitchell and Lima 2002; Schmidt and Ostfeld 2003).

The movement trajectory of individuals represents the outcome of an interaction between
475 behavior and landscape structure (Wiens et al. 1993; Turchin 1998; Morales 2002). Recent
developments in spatial ecology highlights the importance of the size and shape of redistribution
kernels (Kot et al. 1996; Lewis 1997; Keeling et al. 2000; Murrell and Law 2000; Law et al.
2003). However, despite the “productive union” between landscape ecology and behavioral
sciences anticipated by (Lima and Zollner 1996), very little is known about how landscape
480 heterogeneity affects the characteristics of movement patterns (Morales 2002). A common
modeling approach is to investigate the performance of individuals simulated in various
landscapes using predefined movement rules (Turner et al. 1994; Farnsworth and Beechman
1999; Zollner and Lima 1999). Here we tested a different approach, where a combination of
neural networks and genetic algorithms allowed rules to emerge from fitness-related decisions
485 that considered complex array of potential stimuli. This approach, together with summaries of
larger-scale movement properties out of fine-scale behavioral decisions could be useful to

understand the connection between landscapes and animal movement and ultimately in scaling from individuals to populations in heterogeneous landscapes.

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Figure Captions

Figure 1.

500 Schematic representation of the general model structure. The solid boxes represent the four artificial neural networks used to model elk behavioral decisions. **Switch-ANN** decides whether to explore or to forage and for how long to forage. **Diet-ANN** chooses what to eat. **Foraging-Move-ANN** decides where to go while foraging, and the **Exploratory-Move-ANN** chooses where to go while exploring. Inputs to the neural networks are gut content at time of day τ $G(\tau)$,
 505 average neutral detergent fiber in gut at τ $G_{\text{NDF}}(\tau)$ time of day (τ), Julian day J , fat reserves at current day $F(t)$. Plant biomass (Q), predation risk (R) and changes in elevation (ΔH) are perceived either at current position (e.g. $Q(x,y)$), in all neighboring landscape cells (e.g. Q_{1-3}), and under hierarchical perception (e.g. Q_{h1-h3}).

510 Figure 2.

General structure of the Artificial Neural Networks used to model behavioral decisions. An input layer (ϕ) represents the information perceived by the ANN and there is a node (neuron) for each variable. The input nodes are fully connected to a layer of hidden nodes (h). The strength of each connection is given by a matrix of weights ($W_{\phi h}^1$). The values coming into each hidden node are
 515 added together and then transformed to values between minus one and one with a sigmoid

function: $h_i = 1 - 2 / (1 + \exp\left(2 \sum_j W_{ij}^1 \phi_j\right))$, where h_i is the firing intensity of the i -th hidden node

and there are J input nodes. The hidden layer is then fully connected to an output layer (y) and again, the strength of the connections is given by a weight matrix (W_{hy}^2). The values coming to an output node are added and then transformed to a value between zero and one with a sigmoid

520 function $y_i = 1 - 1 / (1 + \exp\left(2 \sum_k^K W_{ik}^2 h_k\right))$. Output values are then translated to some behavioral
 reaction such as movement in a particular direction.

Figure 3. Changes in average population fitness (measured as body fat (kg) before winter times
 survival probability due to predation) with the number of simulated generations for the
 525 homogeneous landscape (solid line), patchy landscape (dotted line), and upper foothills of
 Alberta (dashed line).

Figure 4. Histograms of daily displacements (A-C), and angle histograms (D-F) for movement
 paths in different landscapes. Notice different scales for the displacement histograms.

530

Figure 5. Mean Squared Displacement in different landscapes in (A) homogeneous landscape,
 (B) patchy landscape with predation risk, (C) upper foothills of Alberta. Dotted lines are values
 for all simulated individuals combined. Thick lines are for individuals in the lower 10% of the
 distribution of fitness and the thicker line is for those in the upper 10%. For each landscape we
 535 show a randomly chosen example of a movement path (D-F).

Figure 6. Changes in redistribution kernels with time. Confidence intervals for scale and shape
 parameters of Weibull distributions fitted to the displacement distance (R_n , net distance from
 release point and location at day n) for (A) homogeneous landscape, (B) patchy landscape with
 540 predation risk, (C) upper foothills of Alberta.

Figure 7. Quantile-quantile plot for (A) daily distance moved and (B) turning angles (degrees).

Observed data came from the daily relocation of 8 female elk in Alberta and the simulated data from 100 simulated elk on landscape maps of the upper foothills of Alberta.

545

Figure 8. Net squared displacement for (A) randomly chosen simulated elk in upper foothills of Alberta, and (B) data from a randomly chosen female elk from Alberta.

550

Figure 1.

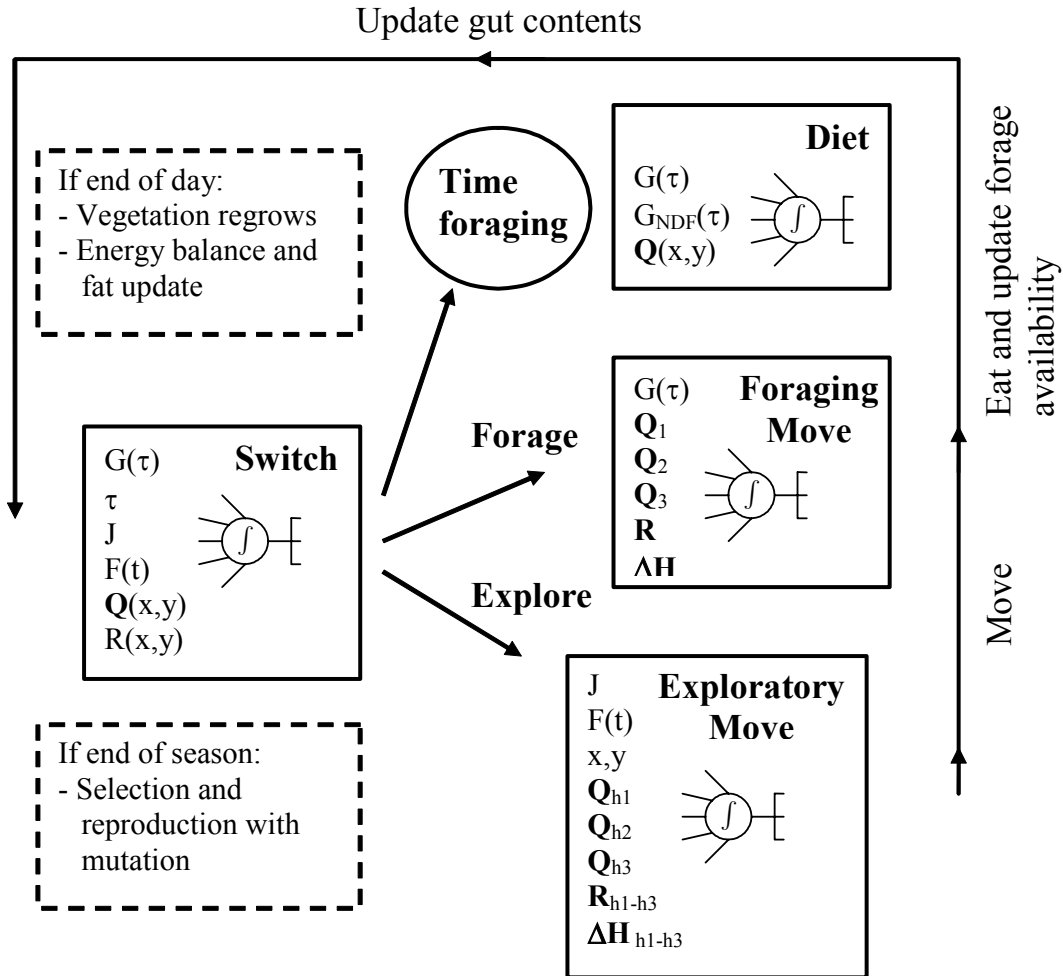


Figure 2.

555

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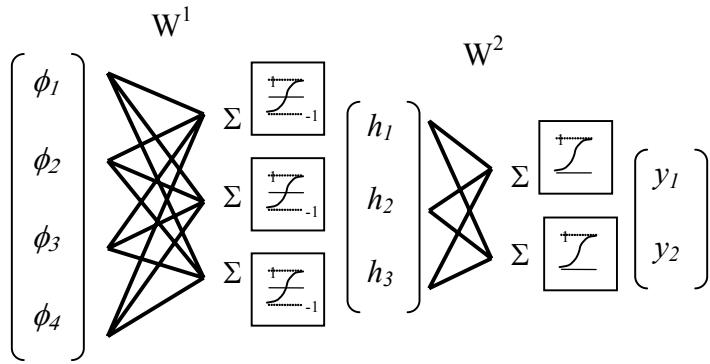


Figure 3.

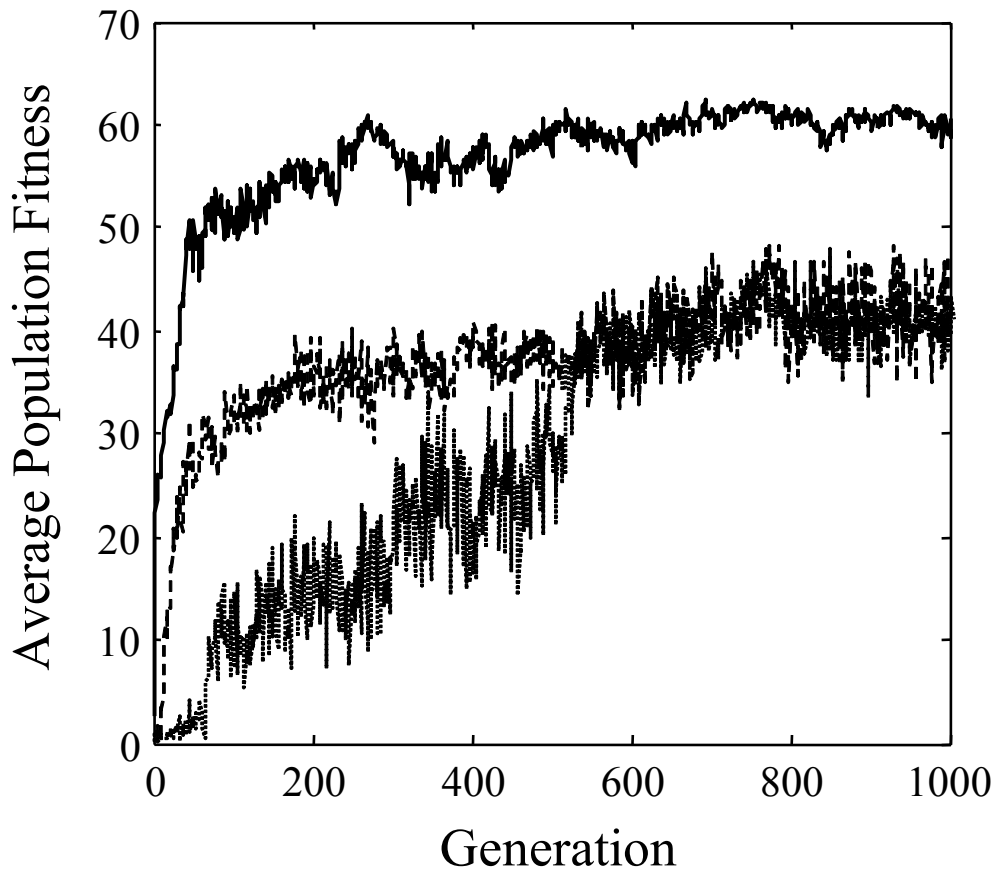


Figure 4.

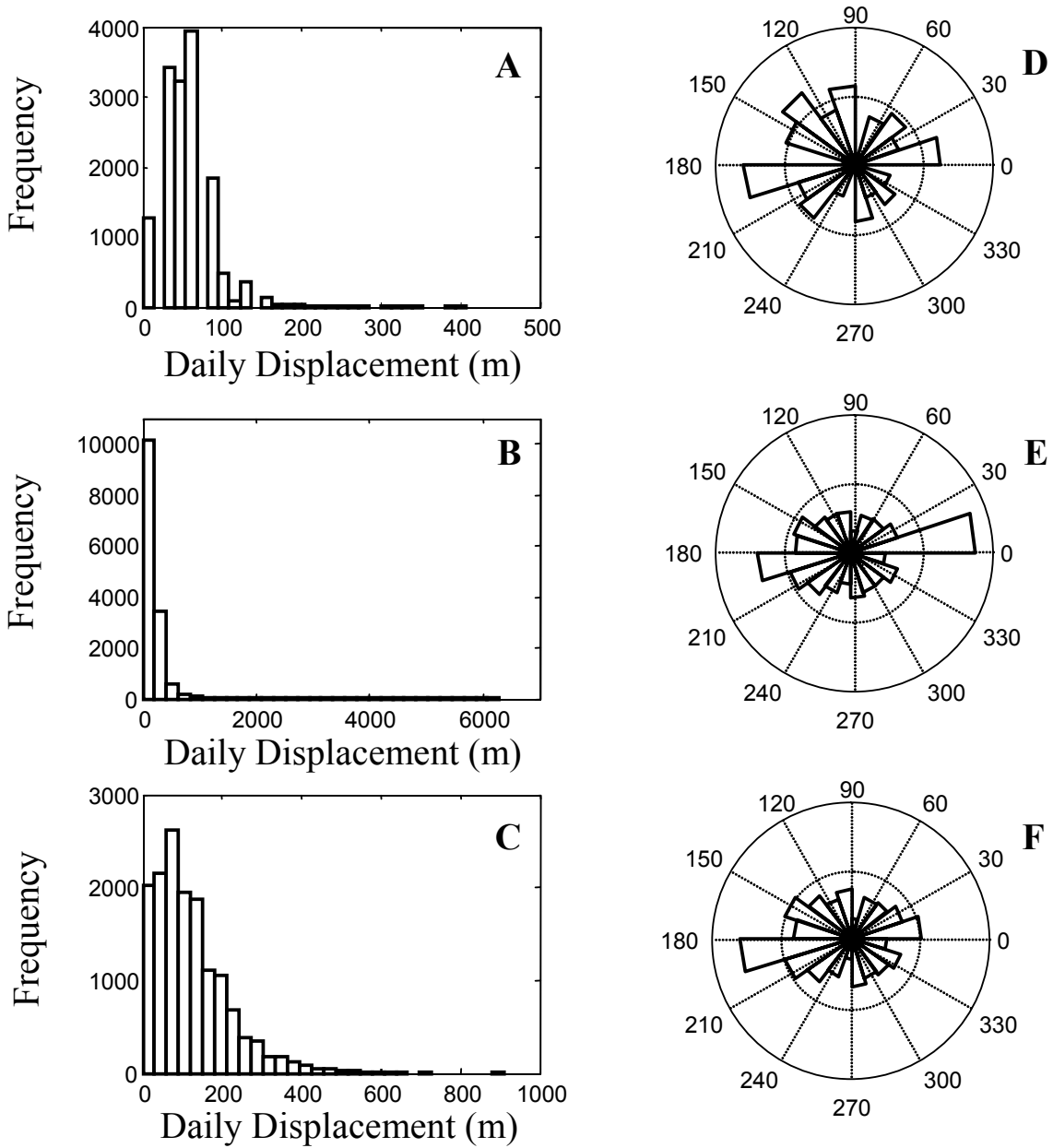


Figure 5.

565

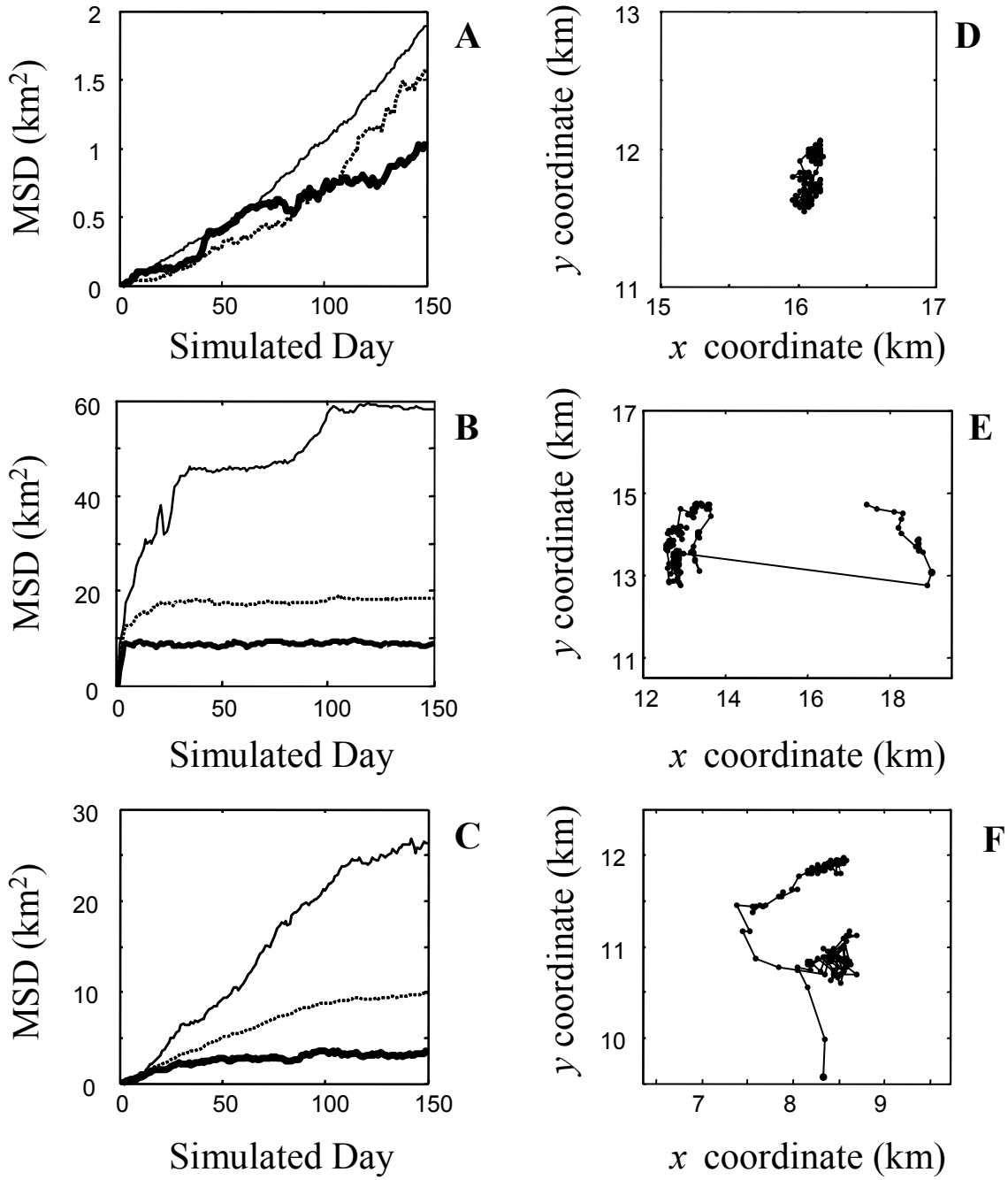


Figure 6.

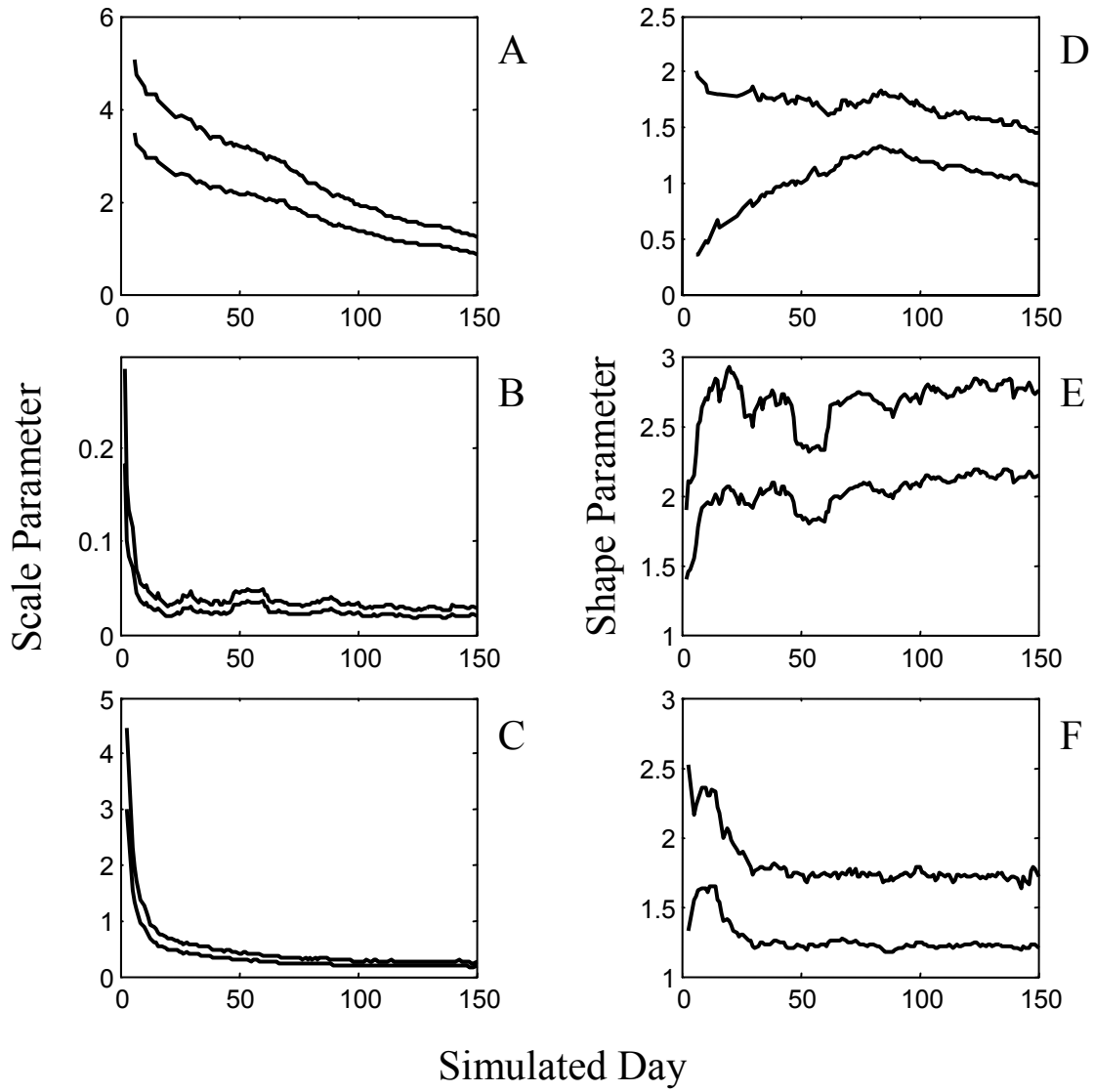


Figure 7.

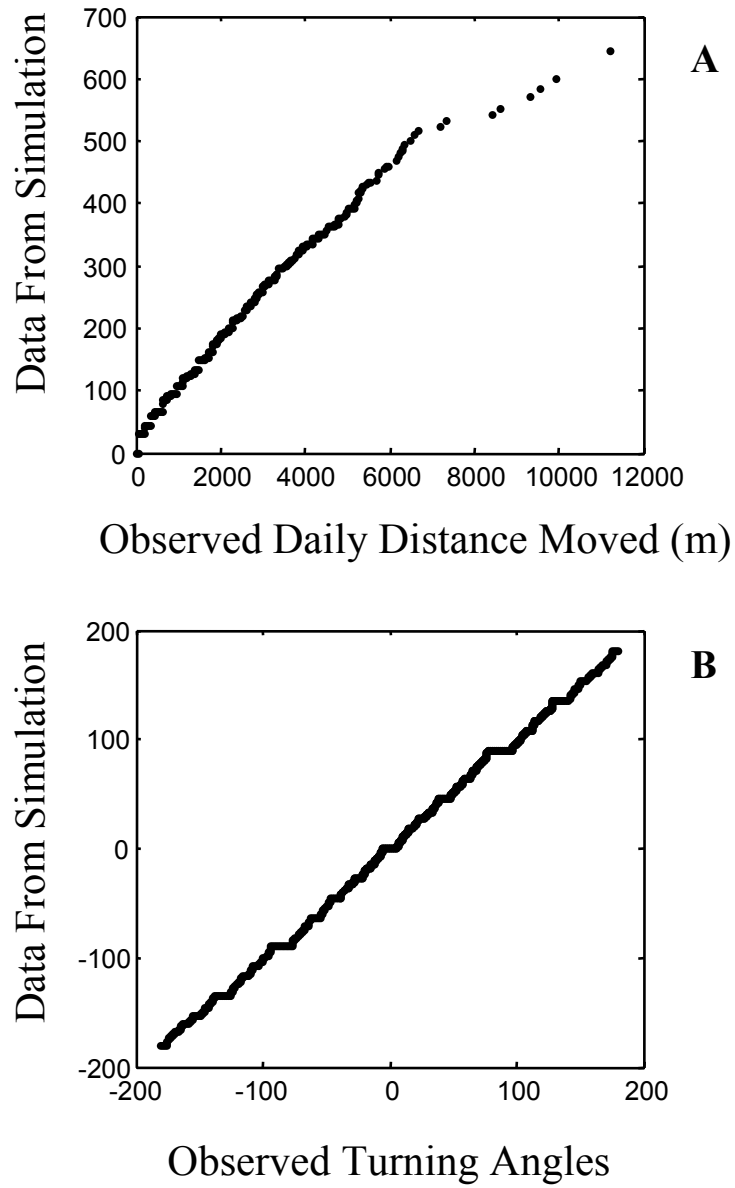
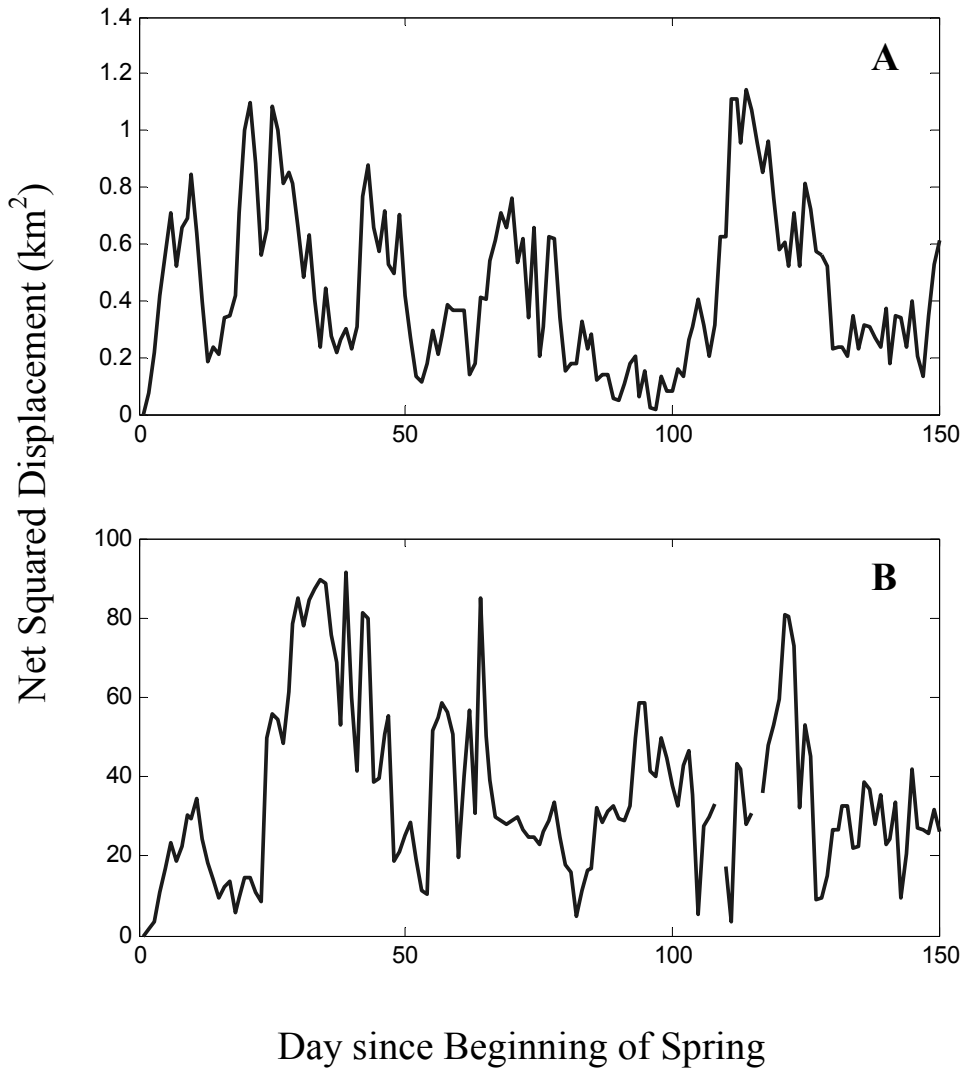


Figure 8.



580 **References**

Adler P.B., Raff D.A. and Lawenroth W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465-479.

Anderson J.A. 1995. An introduction to neural networks. MIT Press, Cambridge, Massachusetts, USA.

585 Bailey D.W., Gross J.E., Laca E.A., Rittenhouse L.R., Coughenour M.B., Swift D.M. and Sims P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386-400.

Beecham J.A. and Farnsworth K.D. 1998. Animal foraging from an individual perspective: an object orientated model. *Ecological Modelling* 113: 141-156.

590 Belovsky G.E. 1984. Herbivore optimal foraging: a comparative test of three models. *American Naturalist* 124: 97-115.

Bergman C.M., Fryxell J.M. and Gates C.C. 2000. The effect of tissue complexity and sward height on the functional response of Wood Bison. *Functional Ecology* 14: 61-69.

Bolker B. and Pacala S.W. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology* 52: 179-197.

595 Cain M.L. 1991. When do treatment differences in movement behaviors produce observable differences in long-term displacements? *Ecology* 72: 2137-2142.

Cook J.G. 2002. Nutrition and food. In Toweill D.E. and Thomas J.W. (eds), *North american elk: Ecology and management*. pp. 259-349. Smithsonian Institution Press, Washington, USA.

600 Cook R.C., Cook J.G. and Mech L.D. 2004. Nutritional condition of northern Yellowstone elk. *Journal of Mammalogy* 85: 714-722.

Delgiudice G.D., Moen R.A., Singer F.J. and Riggs M.R. 2001. Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988.

Wildlife Monographs 147: 1-60.

605 Dieckmann U., Law R. and Metz J.A.J. 2000. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, U.K.

Farnsworth K.D. and Beechman J.A. 1999. How do grazers achieve their distribution? a continuum of models from diffusion to the ideal free distribution using biased random walks. American Naturalist 153: 509-526.

610 Farnsworth K.D. and Illius A.W. 1996. Large grazers back in the fold: Generalizing the prey model to incorporate mammalian herbivores. Functional Ecology 10: 678-680.

Fortin D. 2002. Optimal searching behaviour: the value of sampling information. Ecological Modelling 153: 279-290.

615 Fortin D. 2003. Searching behavior and use of sampling information by free-ranging bison (*Bos bison*). Behavioral Ecology and Sociobiology 54: 194-203.

Fortin D., Boyce M.S. and Merrill E.H. 2004. Multi-tasking by mammalian herbivores: overlapping processes during foraging. Ecology 85: 2312-2322.

Fortin D., Fryxell J.M. and Pilote R. 2002. The temporal scale of foraging decisions in bison. Ecology 83: 970-982.

620 Frair J.L., Merrill E.H., Beyer H.L., Morales J.M., Visscher D.R. and Fortin D. 2004.

Determining scales of movement by elk (*Cervus elaphus*) and their responses to heterogeneity in forage resources and predation risk. Landscape Ecology.

Fryxell J.M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138: 478-498.

- 625 Fryxell J.M., Greever J. and Sinclair A.R.E. 1988. Why are migratory ungulates so abundant. *American Naturalist* 131: 781-798.
- Goldberg D.E. 1989. Genetic algorithms in search, optimization and machine learning. Addison-Wesley Pub. Co., Reading, Massachusetts. USA.
- Grimm V., Frank K., Jeltsch F., Brandl R., Uchmanski J. and Wissel C. 1996. Pattern-oriented
630 modelling in population ecology. *Science of the Total Environment* 183: 151-166.
- Gross J.E., Shipley L.A., Hobbs N.T., Spalinger D.E. and Wunder B.A. 1993. Functional response of herbivores in food-concentrated patches: Tests of a mechanistic model. *Ecology* 74: 778-791.
- Hudson R.J. and Frank S. 1987. Foraging ecology of bison in Aspen boreal habitats. *Journal of*
635 *Range Management* 40: 71-75.
- Hudson R.J. and White R.G. 1985. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.
- Huse G. and Giske J. 1998. Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* 37: 163-178.
- 640 Huse G., Strand E. and Giske J. 1999. Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* 13: 469-483.
- Illius A.W. and Gordon I.J. 1987. The allometry of food Intake in grazing ruminants. *Journal of Animal Ecology* 56: 989-999.
- Illius A.W. and Gordon I.J. 1992. Modelling the nutritional ecology of ungulate herbivores:
645 evolution of body size and competitive interactions. *Oecologia* 89: 428-434.
- Jiang Z. and Hudson R.J. 1992. Estimating forage intake and energy requirements of free-ranging wapiti *Cervus-elaphus*. *Canadian Journal of Zoology* 70: 675-679.

- Johnson C.J., Parker K.L., Heard D.C. and Gillingham M.P. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* 71: 225-235.
- 650 235.
- Jung H.G. and Koong L.J. 1985. Effects of hunger satiation on diet quality by grazing sheep. *Journal of Range Management* 38: 302-305.
- Kareiva P. and Odell G. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. *American Naturalist* 130: 233-270.
- 655 Keeling M.J., Wilson H.B. and Pacala S.W. 2000. Reinterpreting space, time lags, and functional responses in ecological models. *Science* 290: 1758-1761.
- Kot M., Lewis M. and van den Driessche P. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77: 2027-2042.
- Law R., Murrell D.J. and Dieckmann U. 2003. Population growth in space and time: spatial logistic equations. *Ecology* 84: 252-262.
- 660 252-262.
- Lewis M.A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. In Tilman D. and Kareiva P. (eds), *Spatial ecology: the role of space in population dynamics and interspecific interactions*. pp. 46-69. Princeton University Press, Princeton, New Jersey, USA.
- 665 Lewis M.A. and Murray J.D. 1993. Modelling territoriality and wolf-deer interactions. *Nature* 366: 738-740.
- Lima S.L. and Zollner P.A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11: 131-135.
- McNaughton S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *American*
- 670 *Naturalist* 124: 863-886.

- Mitchell M. and Forrest S. 1995. Genetic algorithms and artificial life. In Langton C.G. (ed), Artificial life: an overview. pp. 267-289. MIT Press, Cambridge, Massachusetts, USA.
- Mitchell W.A. and Lima S.L. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos* 99: 249-259.
- 675 Moen R., Pastor J. and Cohen Y. 1997. A spatially explicit model of moose foraging and energetics. *Ecology* 78: 505-521.
- Morales J.M. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. *American Naturalist* 160: 531-538.
- Morales J.M. and Ellner S.P. 2002. Scaling up movement in heterogeneous landscapes: the
680 importance of behavior. *Ecology* 83: 2240-2247.
- Morales J.M., Haydon D.T., Frair J., Holsinger K.E. and Fryxell J.M. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 89: 2436-2445.
- Murrell D.J. and Law R. 2000. Beetles in fragmented woodlands: a formal framework for
685 dynamics of movement in ecological landscapes. *Journal of Animal Ecology* 69: 471-483.
- Parker K.L., Robbins C.T. and Hanley T.A. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48: 474-488.
- Pastor J., Moen R. and Cohen Y. 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. *Journal of Mammalogy* 78: 1040-1052.
- 690 Robbins C.T. 1993. Wildlife feeding and nutrition, second edition. Academic Press, San Diego, California, USA.
- Schmidt K.A. and Ostfeld R.S. 2003. Mice in space: Space use predicts the interaction between mice and songbirds. *Ecology* 84: 3276-3283.

- 695 Schmitz O.J., Beckerman A.P. and O'Brien K.M. 1997. Behaviorally mediated trophic cascades:
Effects of predation risk on food web interactions. *Ecology* 78: 1388-1399.
- Shipley L.A., Spalinger D.E., Gross J.E., Hobbs N.T. and Wunder B.A. 1996. The dynamics and
scaling of foraging velocity and encounter rate in mammalian herbivores. *Functional Ecology*
10: 234-244.
- 700 Spalinger D.E. and Hobbs N.T. 1992. Mechanisms of foraging in mammalian herbivores: new
models of functional response. *American Naturalist* 140: 325-348.
- Strand E., Huse G. and Giske J. 2002. Artificial evolution of life history and Behavior. *American
Naturalist* 159: 624-644.
- Tilman D. and Kareiva P., (eds). 1997. *Spatial ecology: the role of space in population dynamics
and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- 705 Turchin P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population
Redistribution in Animals and Plants*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Turchin P. and Batzli G. 2001. Availability of food and the population dynamics of arvicoline
rodents. *Ecology* 82: 1521-1534.
- 710 Turner M.G., Wu Y., Romme W.H. and Wallace L.L. 1993. A landscape simulation model of
winter foraging by large ungulates. *Ecological Modelling* 69: 163-184.
- Turner M.G., Wu Y., Wallace L.L., Romme W.H. and Brenkert A. 1994. Simulating winter
interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological
Applications* 4: 472-496.
- 715 Whitley D. 2001. An overview of evolutionary algorithms: practical issues and common pitfalls.
Information and Software Technology 43: 817-831.

Wiens J.A., Stenseth N.C., Van Horne B. and Ims R.A. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66: 369-380.

Wilmshurst J., Fryxell J. and Hudson R. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* 6: 209-217.

720 Wilmshurst J.F., Fryxell J.M. and Bergman C.M. 2000. The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London, Series B* 267: 345-349.

Zollner P.A. and Lima S.L. 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80: 1019-1030.

725

Appendix 1

Mixed diet functional response

We assume that plant types are intermingled, and have an overall uniform distribution within a
 730 pixel. Herbivores crop each food item in one bite and, while chewing this vegetation, they travel
 directly to the next item at speed of V_{max} (60 m/min for elk, Shipley et al. 1996). Plants of type i
 are accepted in the diet in a proportion γ_i (range: 0-1) of their encounter rate. The values of γ_i
 correspond to the output of the **Diet-ANN** and are influenced by food availability and internal
 conditions. Certain food items may end up being always, never or sometimes consumed by the
 735 forager upon encounter. Under these assumptions, searching herbivores encounter food items at
 a rate

$$\lambda_{tot} = V_{max} \sum_i^N \sqrt{D_i} \gamma_i \quad (\text{A.1})$$

where λ_{tot} (plant/min) is total encounter rate and D_i is the density of plants (number of plants per
 m²) of the i -th, out of N , type. The short-term rate of vegetation intake (I , g/min) can be
 740 controlled either by the rate of food handling in the mouth (cropping and chewing) or by the
 encounter rate with food items (Spalinger and Hobbs 1992; Farnsworth and Illius 1996; Fortin et
 al. 2002). When forage intake rate is limited by handling rate (foraging process 3, Spalinger and
 Hobbs 1992), the time spent chewing the current food item exceeds (or is exactly equal to) the
 time required to encounter the next food item. That is, the consumption of food type i relates to
 745 process 3 whenever:

$$1/\lambda_{tot} \leq P_i/R_{max} \quad (\text{A.2})$$

where R_{max} (47.41 g/min for elk, Gross et al. 1993) is the amount of food that can be chewed
 each minute in absence of cropping (Spalinger and Hobbs 1992). If we refer to the smallest plant

for which equation A.2 holds as a plant of type u , the proportion of foraging time where food
 750 intake is controlled by process 3 (α) is given by:

$$\alpha = \frac{\sum_{i=u}^N \sqrt{D_i} \gamma_i}{\sum_{i=1}^N \sqrt{D_i} \gamma_i} \quad (\text{A.3})$$

During process 3 of foraging, the rate of food intake of a given plant can be found by dividing its
 size by the time required to handle (crop and chew) that plant (Gross et al. 1993):

$$I^{proc3} = \frac{P}{\bar{h} + P/R_{\max}} = \frac{R_{\max} P}{R_{\max} \bar{h} + P} \quad (\text{A.4})$$

755 where \bar{h} (0.015 min/plant for elk, (Gross et al. 1993)) is time require to crop an individual plant.
 Expanding this equation to provide the average I for foragers consuming all plants as large or
 larger than P_u , we get:

$$I^{proc3} = \frac{R_{\max} \sum_{i=u}^N \sqrt{D_i} \gamma_i P_i}{R_{\max} \bar{h} \sum_{i=u}^N \sqrt{D_i} \gamma_i + \sum_{i=u}^N \sqrt{D_i} \gamma_i P_i} \quad (\text{A.5})$$

When individuals consume plants smaller than P_u , the rate of food intake is limited by encounter
 760 rate with food items which, given our assumptions (see above), corresponds to a process 2 of
 foraging (sensu Spalinger and Hobbs 1992). During process 2, I can be found by dividing the
 size of a plant by the time require to crop that plant and travel to the next food item:

$$I^{proc2} = \frac{P}{\bar{h} + 1/V_{\max} \sqrt{D}} = \frac{V_{\max} \sqrt{D} P}{1 + \bar{h} V_{\max} \sqrt{D}} \quad (\text{A.6})$$

This equation can be expanded to provide the average energy intake rate during foraging
 765 situation 2 by considering the average size of the plants smaller than P_u (i.e., plants for which Eq.
 A.2 does not hold) and the time required to reach the next food item:

$$I^{proc2} = \frac{V_{\max} \sum_{i=1}^{u-1} \sqrt{D_i} \gamma_i P_i \sum_{i=1}^N \sqrt{D_i} \gamma_i}{V_{\max} \bar{h} \sum_{i=1}^{u-1} \sqrt{D_i} \gamma_i \sum_{i=1}^N \sqrt{D_i} \gamma_i + \sum_{i=1}^{u-1} \sqrt{D_i} \gamma_i} \quad (\text{A.7})$$

Because an entire spectrum of plant size can be found each pixel, herbivores may experience both foraging processes (i.e., process 2 and process 3). The overall instantaneous food intake rate

770 within a pixel thus corresponds to $I = \alpha I^{proc3} + (1-\alpha) I^{proc2}$.