3.13.2 Spatial extensions

The Climate, Soil and Vegetation modules were duplicated in each cell of a grid. This method was implemented as inheritance of the non-spatial *Climate*, *Soil* and *Plant* classes (Derry 1998) by extended hierarchies that incorporated spatial features (see Appendix 6), distributed across a grid. The result was that each spatial class contained a grid of equivalent dimensions (*I* columns by *J* rows, and each cell had co-ordinates (i,j), where $i \in \{1,\ldots,I\}$ and $j \in \{1,\ldots,J\}$), rather than the alternative of a single grid containing many spatial classes. The benefit was that during the introduction of spatial features (*e.g.*, cell altitude with which to generate a topographic landscape), module integrity was more easily maintained. For example, within grid communication such as runoff to neighbouring cells is a process occurring at the soil surface and was, therefore, coded for within the *Soil* module. Individual cells were referenced using the co-ordinate system, while whole grid data was collected by systematic contiguous sampling (*i.e.*, in sequence from top left corner, column-by-column).

Herbivore species were able to access the extent of the modelled area, therefore only one instance of each *Herbivore* class was required. However, a grid-based implementation of the existing diet selection object pointer method (see Derry 1998) was introduced by which selection of a spatially distributed diet and the associated herd movement could be predicted on a daily basis.

3.13.3 Scale issues

It is imperative to consider scale issues when modelling ecological systems (Wu & Hobbs 2002, Chave & Levin 2003). Many problems that may have hindered the development of this model were avoided by tracking most state variables in terms of density per unit area. Only the *Animal* module dealt in absolute values. For example, selected plant biomass was converted from a measure of dry matter density (kg DM/ha) to absolute biomass (kg DM) in order to calculate total herd consumption. Animal populations comprised age classes tallied by their total membership, but population

dynamics were expressed in terms of animal density: animals per unit area (see Section 3.13.12).

Animal decisions are thought to conform to spatial scales; region, landscape and plant community (Senft *et al.* 1987). Bailey *et al.* (1996) extended this framework and proposed an attractive conceptual model of animal spatial foraging that involved selection down a hierarchy of six spatial (and temporal) scales; home range (1 month to 2 years), camp (1-4 weeks), feeding site (1-4 hours), patch (1-30 minutes), feeding station (5-100 seconds) and bite (1-2 seconds). Thus, selection at the habitat scale is a decision made prior to subsequent foraging decisions at smaller scales (Orians & Wittenberger 1991, Adler *et al.* 2001). The defining levels of this hierarchy are dictated by the size of the animal, because species of different size perceive the environment differently (Wiens 1976). This also defines the scale of patchiness for the animal's environment, and, it follows, the selectivity of their resource (Wallis De Vries *et al.* 1999). The sequence is attractive because it is not dissimilar to the sequence of decisions that we ourselves may follow in our own foraging excursions. Supermarket (5-10 minutes) → aisle (1-2 minutes) → shelf (1-30 seconds) → item category (1-5 seconds) → item (1-2 seconds). Or perhaps, restaurant (10-30 minutes) → table (5-10 minutes) → menu (1-10 minutes) → course choice (1-5 minutes) → dish choice (1-2 minutes). But, in other species, this remains a conceptual framework and there is little empirical evidence in its support. Animal diet selection can be influenced by the fine scale distribution of their food resources (Edwards *et al.* 1994, Turner 1999), but, it is much more difficult to establish selection at the scale of the habitat (feeding site *sensu* Bailey *et al.* 1996). One such example is provided by Fritz *et al.* (1996), who found selection of certain habitats (300 ha paddocks) by impala and kudu disproportionate to their availability (by area). However, they could only conclude that selection had been at the scale of individual species within those habitats, rather than, say, for habitat-defining plant communities. This is in accord with further evidence for random or nearest-neighbour search strategies with little or no active habitat selection (Turner *et al.* 1993, Gross *et al.* 1995, Forcadi *et al.* 1996 and Chapter 2). Because the animal herd moved

from cell-to-cell, selection in the model was ultimately for the area represented by each grid cell (*see below*). But, the selectivity of animals for each cell was determined at the finer spatial scale of plant part density, with assessment of larger areas being based simply on mean accumulated resource profitability.

A daily iteration was chosen for the model. Although quicker processes are modelled (*e.g.*, animal movement between cells), energy fluxes were tallied at the end of each simulated day. Thus, a smaller temporal scale would not have enabled any more precision, whereas a longer iteration period (not just summation across days) would have denied investigation of daily foraging bouts (including animal digestive constraints, see below). The SAVANNA model (Coughenour 1993) employed a weekly time step, but the model aggregated daily rates and then merely reapportioned animal foraging days per grid cell according to a preference score. It is possible that a longer time step for the current model would have reduced simulation time.

3.13.4 Energy intake

Herbivores select their diets from a wide range of plants. The size of the animal typically determines their feeding behaviour (Illius & Gordon 1987). Buccal characteristics scale allometrically with body mass, the smaller animal having a narrower snout, which can be used to probe plant morphology (Gordon & Illius 1988). Therefore, depending on body size, the animal is able to select parts from within each plant. The reason for doing this is because plant parts differ in their nutritional value, which is related to a part's digestibility, a function of its nitrogen content (Illius *et al.* 1996a). Hence, upon maturation of plant parts, replacement of the nitrogen-rich cell contents by plant secondary thickening carries with it an associated reduction in digestibility (Illius *et al.* 1996a).

Digestibility is an important factor in energy intake. The digestible portion of consumed forage is that part that can be absorbed by the animal and is not excreted as fæces. Increased digestibility means less rumen fill, higher throughput and, therefore, more