

total intake by reduction of digestive constraints on intake (McDonald *et al.* 1977). The maximum intake of food was predicted with respect to its digestibility and animal size (Illius & Gordon 1991, 1992). Constant digestibility values for each plant part were included in the model. As the animals were able to select from a mixture of dietary components, the daily digestibility was an average of the plant part digestibilities weighted according to their contribution to daily intake (Fig. 3.4, see Section 3.13.12 for parameter values).

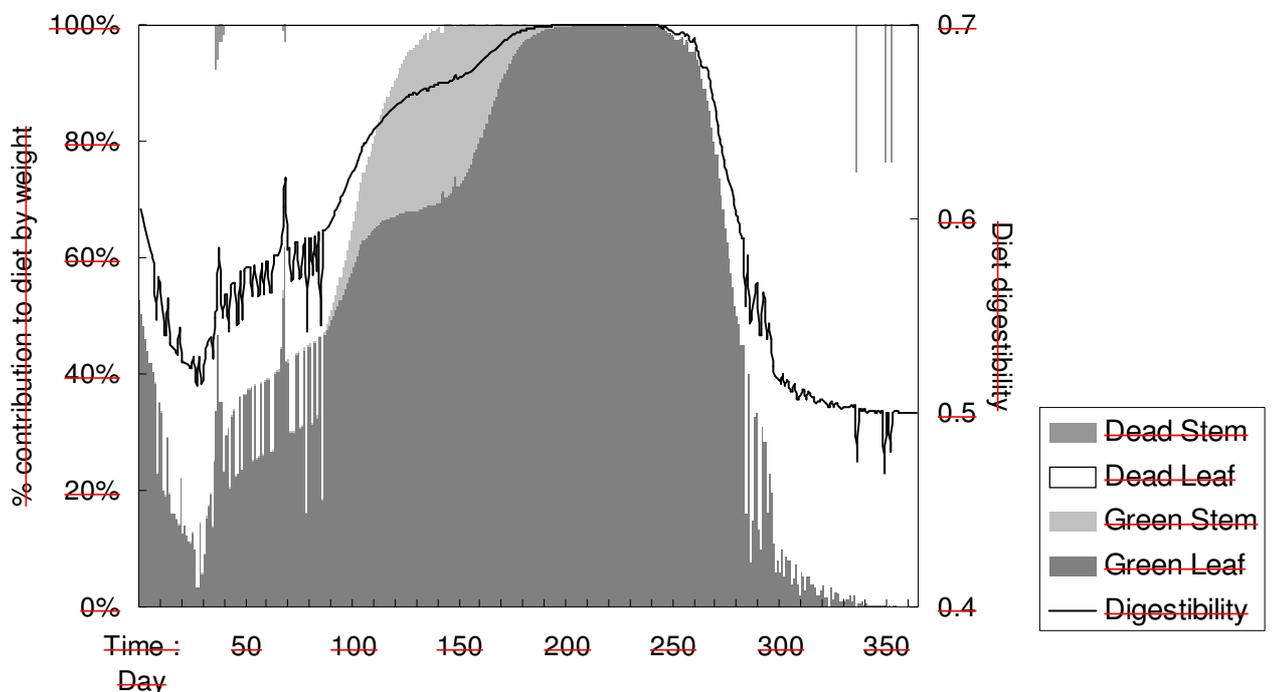


Fig. 3.4: Typical annual seasonal change in modelled herbaceous diet composition and the resulting digestibility for goats selecting parts of a perennial grass. *Dead stem* appears as the thin drop-down bars at the top of the figure.

### 3.13.5 Spatial foraging

Field observations and modelling exercises have shown that the maximization of daily energy gain is the rationale for optimal foraging strategies (Fryxell *et al.* 2001) and the

primary determinant of animal movement patterns (Wilmshurst *et al.* 1999). Goats in particular have been shown to select diets that maximize their dry matter intake rate (Illius *et al.* 1999). Each day, animals foraged until either no available foraging time remained (this accounted for time for the return trip to water during the dry season), or daily intake requirement had been satisfied (see Section 3.13.11).

During the daily iteration, each cell of the *Herbivore* class spatial diet grid was populated with estimates of potential energy intake rate ( $E_{ij}^R$ ,  $\text{J s}^{-1}$ ) for the plant parts of each forage species present in that cell. This was predicted allometrically from the mass of a mature female animal. These intake rates were then processed using the extended contingency model of Farnsworth & Illius (1996, 1998, but also Fortin 2001), to account for simultaneous searching and handling of multiple prey items. The process involved separate addition of individual items to a mixture of plant components until the diet mix became handling-limited for the food item offering the highest profitability. Lower quality food items were discarded on the assumption that they would not increase the diet's energy intake rate, apart from a sufficiency to fill the animal's remaining gut capacity.

In this way optimal diets could be selected from each diet cell combining plant parts belonging to any number of forage species. As the spatial diet pointer grid was particular to each herbivore species, grids could differ between species according to animal size. Finally, actual intake was predicted by selection of a daily pathway that maximized energy intake. The complete optimal solution is akin to the Travelling Salesman Problem, however as it is unlikely that animals make decisions about movement in this way (Beecham & Farnsworth 1998), a stepwise sequential solution was favoured for realism.

Herd movements were driven by there being an available cell destination (see below). If a destination did not exist, the herd did not move. The herd moved when cued by sufficient depletion of forage resources at the current cell location. The theoretical

giving up density, GUD, (*i.e.*, the resource density remaining when there is no profit in staying) is widely accepted as the point at which depletion of the current location depresses the resource to  $G^*$ , the environmental (global) mean  $E_{ij}^R$  (a derivative of the Marginal Value Theorem, Charnov 1976). The central assumption here is that enough knowledge about the environment has been collected in order to make the comparison. In accordance with the IFD, typically animals are considered to have perfect knowledge of their environment, as if omniscient, or having permanent retention of encounters with resource profitability throughout their foraging range. Density-dependent interference effects were not included.

Before moving to a cell, the destination cell needed to be deemed profitable. For a cell to be profitable  $E_{ij}^R$  needed to be sufficient to account for the costs of travel to the cell, *i.e.*, commuting ( $E_{ij}^C$ , J), plus the costs of travel within the cell required to harvest the selected diet, *i.e.*, foraging ( $E_{ij}^F$ , J), at a potential energy intake rate above  $G^*$ . This gave the cell net potential energy intake rate,  $e_{ij}$  (Equation 3.5).

$$e_{ij} = E_{ij}^R - E_{ij}^C - E_{ij}^F - \left( \sum_i \sum_j E_{ij}^R \right) / IJ \quad 3.5$$

Time and energy foraging costs were calculated from the cell  $e_{ij}$  and the distance travelled whilst foraging, which was a function of bite size and bite density. Animals were assumed to commence foraging at the centre of each cell and forage towards the next destination. Therefore the distance commuted to a cell centre was assumed to be the actual distance between the cell centres less the distance travelled whilst foraging in the previous cell. Time and energy commuting costs were calculated from commuting distance using an estimate of herd velocity, which was weighted according to herd composition (O'Brian 1984).

Thus animal movement was not randomized. Random walk models (*e.g.*, Stafford Smith 1990, Renshaw 1991) and diffusion models (*e.g.*, Blackwell 1997, Farnsworth & Beecham 1999) imply that, in the absence of experimental evidence, a stochastic mechanism underlies animal foraging behaviour. However, recent empirical findings, including the fieldwork presented in Chapter 2, show that nearest-neighbour models may best describe movement patterns. In so doing, there is the suggestion that it is the aggregation of individual plants that provides the correlation required to transform random walk models into successful animal foraging strategies, with the optimal degree of correlation inversely proportional to patch density (Zollner & Lima 1999). Thus, browsing animals have been observed to follow tortuous foraging paths through dense habitats but travel more directly and quicker between sparsely spaced bushes (Etzenhouser *et al.* 1998). Animals improve their foraging efficiency with alternative search patterns for different levels of the hierarchical patch system (Fauchald 1999). Whilst the most effective non-systematic search paths are almost straight, an animal with a superior perceptual range is able to elicit similar foraging success from an exhaustive search strategy (Zollner & Lima 1999). So, good sight would be an advantage in sparsely vegetated areas, for the identification of patches in terms of forage species (Illius *et al.* 1999), but susceptible to impedance by physical barriers in denser areas (Etzenhouser *et al.* 1998). The model measures resource patchiness using the CV<sup>1</sup> for  $E_{ij}^R$  and assumes that vision is not impeded within the visual range.

### **3.13.6 Vision**

~~Considering the difficulties in taking such measurements, it is not surprising that there is little empirical evidence for visual range in large herbivores. More has been achieved using visual cues in studies of spatial memory and foraging efficiency. Howery *et al.* (1999) found that artificial visual cues increased foraging activity and improved intake under fixed and variable forage arrangements. The arena that was used measured 1.58 acres (0.64 ha) which is equivalent to ~80 m maximum visual range. Laca & Ortega~~

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<sup>1</sup> coefficient of variation