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[1] 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

---

[1] coefficient of variation

(1996) also investigated the role of visual cues in spatial foraging by its effect on cattle intake rate, but their experimental range only reached 23 m. Spatial memory in sheep was tested in paddocks no larger than 45 m (Edwards *et al.* 1996) and 65 m (Edwards *et al.* 1997).

The positioning of the eyes on the head is paramount in deciding the animal's field of vision. This is how much can be seen without moving the head. For humans this is about 180° laterally. For a horse it is about 215° (Ramel 2004). A wide field of vision is characteristic of ungulates and may be an adaptation by prey animals to enable early detection of predators (Walls 1942 cited in Hutson 2000). As this is common in ungulates, it seems reasonable to base an estimate of visual range upon this characteristic. To minimize the constraints of this estimate it also seems reasonable to make this an optimistic estimate at the maximum known abilities of ungulate vision.

The location of ocular orbits on the side of the ungulate skull limits binocular vision, but enhances the animal's field of view or peripheral vision. However, their monocular vision means they can see an object with only one eye, each eye having a field of view of almost 180°. Therefore, by using both eyes, these animals almost have a 360° field of view (Smythe 1975). In some herbivores there is some overlap in the field of view and these animals may have partial binocular vision (Sullivan 1999). Piggins and Phillips (1996) recorded a 306° field of vision in sheep, where ears, horns and wool obstructed a greater panoramic vision. Estimates of field of vision in cattle range from 330° (Phillips 1993) to nearly 360° (University of California Cooperative Extension 1996).

Clark & Dukas (2003) presented this probabilistic detection function for predator vigilance in a foraging animal with field of vision θ,

$$f(\theta) = \delta_0 e^{-\theta/a} \qquad\qquad 3.6$$

where, δ_0 (m) is visual acuity or range, and a is attentional capacity, used in their model to impose limitations on perception and test the importance of cognitive constraints. This is not the purpose of the current model, so the equation was rearranged for δ_0, and f(θ) and a were set to their maximum values. Taking the midpoint between the two literature estimates for θ of 330° and 360° gives 345° which, using the rearranged Equation 3.6, gives a visual range of ~400 m. This value for the animals' limit of perception was used in the model for animal assessment of their resource landscape. The effect of restricting visual range was compared with an equivalent simulation in which vision was unrestricted (see Fig. 3.11).

3.13.7 Assessment

With energy intake rate as fundamental, it was possible to incorporate visual range, the influence of prey species aggregation and nearest-neighbour selection into a vocabulary of animal assessment strategies for optimal landscape utilisation, across increasing scales, in fact, a Herbivore Assessment Lexicon (HAL) (see table 3.7).

To account for influences of patch density the spatial pointer grid was arbitrarily segmented into four directions of travel, such that each sector comprised D_d cells (where $d = 1,2,3,4$). Next, HAL calculated the mean e_{ij} that could be achieved by travel as far as the perceptual limits in each direction (p cells from current). These directional mean values do not acknowledge structural organisation of the landscape into a scale hierarchy of patches or super-patches (*sensu* Beecham & Farnsworth 1988). However, they do take into account the perceivable profitability for clumped resources at remote locations, beyond the scope of neighbouring cells, out to the limits of animal visual range. Taking the sum in these blocks would have given leverage to a larger collection of cells for non-central positions. Next, HAL compared the e_{ij} of the cells neighbouring the current position and having membership of the directional segment with maximum mean e_{ij}. If the search failed to find a profitable cell immediately proximate to the current location, then the search was expanded to the next nearest cells, and so on, until the limits of perception were reached.