

~~It was therefore possible that the first cell visited might not be adjacent to the starting position for the day. Subsequent destinations also may not neighbour previous locations. For depleted landscapes where few profitable cells remained, the constraints on perceptual limit (range and direction) were relaxed, leading to an exhaustive grid-wide search, ranging out in incrementing annuli, from the current location in all directions².~~

3.13.8 Global and local G*

Optimality of foraging strategies was tested by modification of the assumptions made for G*, the environmental mean E_{ij}^R . As mentioned above, global G* was the mean potential energy intake rate calculated for the whole grid. Local G* was calculated as the mean E_{ij}^R of only the cells scanned during assessment as described in Section 3.13.7, above. This also included the cells visited along the foraging path.

Local G* should provide a more accurate estimate of the mean energy intake rate offered by the most available resources at the beginning of each day. During the dry season, animals that assess their environment globally would be expected to travel further from water to reach resource levels in excess of G*. Because local G* is estimated only from previous encounters, for an established utilisation gradient, this estimate would be expected to be lower than global G*.

The grids were initialized with low variation for the spatial distribution of vegetation (CV of only 1%), making starting conditions near identical. Consequently there is little difference between the local and global estimates of G* until the onset of the wet season which introduces more variation via plant growth (Fig. 3.5). Here, the locally derived measure of G* showed erratic fluctuations reflecting a series of encounters with

² ~~An alternative algorithm would have been to invoke a random or correlated random walk for exhausted grids. However, this would not be in keeping with the deterministic algorithm employed, which was purposely based on a nearest-neighbour rule in contrast to random walk models. Random walk models have enjoyed some success, but it was patch density that went some way towards determining animal foraging paths in the model, and it should have been the relaxation of this rule in extreme conditions and not substitution of an unrelated rule.~~

favorable and less profitable patches, but overall was in good agreement with global G^* . The most consistent trend away from global G^* was seen during the dry season after day 240, as available forage declined and profitable cells were sparsely distributed (or located beyond the dry season foraging range). Although the estimate of G^* is pessimistic (lower than the actual environmental mean), animals are unable to reach the profitable resources. Under such conditions, it is no advantage to have knowledge of better sites beyond local depressions in patchy resources as this inflates G^* , and reduces the comparative profitability of local resources accessible during the dry season.

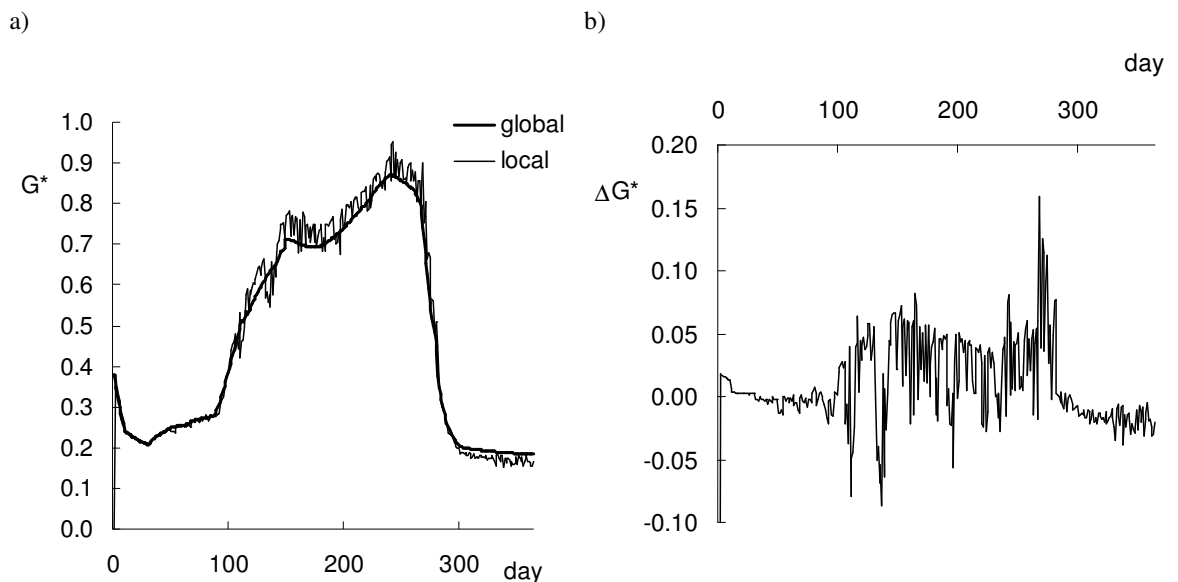


Fig. 3.5: Optimality in foraging strategies for two estimates of environmental mean resource levels. a) globally and locally derived measures of G^* and b) the difference between global and local G^* . The wet season started on day 30 of each year, and ran until the next dry season on day 240

Local G^* would be expected to be an underestimate of global G^* for established utilisation gradients. However, the starting conditions here are almost identical, with nearly homogeneous distributions of initial plant biomass the only potential source of variation. Cells encountered early in both simulations have similar resource levels.

Consequently, there is little difference between the estimates of local and global G^* . Local G^* responded to the wet season increase in resource heterogeneity, and showed signs of departure from global G^* during the second dry season. To investigate the effect of the scale of assessment on optimal foraging behaviour, identical sets of simulations were made for local and global G^* (Fig. 3.9 and Fig. 3.13).

3.13.9 Memory

There is some evidence that implicates learning and memory in reinforcement of visual cues, in goats (Illius *et al.* 1999) and other animals (cattle and sheep: Provenza 1995; sheep: Edwards *et al.* 1996, 1997; Arabian oryx: Tear *et al.* 1997). Derek Bailey and his colleagues have shown that foraging animals retain information gained from their search path and use it to facilitate future diet location (Bailey *et al.* 1989, Bailey 1995, Bailey & Sims 1998, Howery *et al.* 2000). Memory also provides additional information about expected profitability to supplement G^* , thereby combining the global average with recent experience (Hewitson 2002). Memories of both positive and negative encounters are stored (Bailey *et al.* 1996, Hewitson 2002) – these are potential yields above and below what is expected. Negative encounters are remembered for longer than positive, as it is more costly to return to a feeding site that will incur an energetic loss. Using literature values for memory retention capacity in cattle (Bailey *et al.* 1996), memories were decayed with distinct half-life estimates (see Fig. 3.6) according to whether it was worthwhile feeding (the site offered E_{ij}^R above that expected) or not (the potential intake rate was below expectation)³.

The model only has these positive and negative memory feedbacks, and lacks differential retention with respect to scale. For example, Fauchald (1999) showed how

³ A more sophisticated approach is to employ an Exponentially Weighted Moving Average (EWMA, Hunter 1986) model of memory retention in which devaluation of the information is dependent on the rate of change of the environment. This allows the forager to track environmental heterogeneity but involves as yet undocumented species-specific values for the influence of single resource encounters on the running average for remembered resource profitability.