

~~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.

memories related to high encounter rates at small scales are forgotten faster than long-term encounters at large scales.

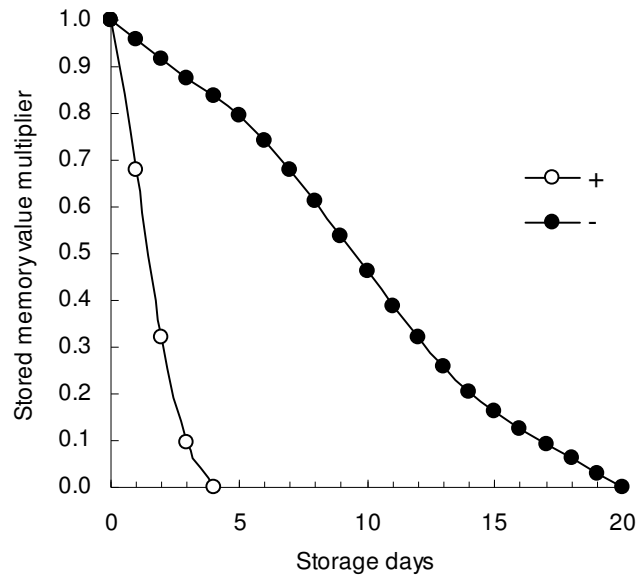


Fig. 3.6: Memory decay functions for stored positive and negative encounters based on literature half-life estimates of 2 days for positive memories and 10 days for negative memories.

Memory was integrated into the assessment of the above mentioned four grid segments as a summative influence underlying the decision, *which direction to travel next*. Thus, for a grid dominated by negative memories, animals are repelled from their latest locations towards less recently visited areas. This occurs mainly during the dry seasons (Fig. 3.7). When resources are more abundant, for most of the wet season, animals are attracted back to recently visited sites. It can be shown that while the number of positive encounters may be relatively high, the effective memory value may be low, depending on the season (*e.g.*, compare first ten days or the latter part of the wet season in Fig. 3.7a and Fig. 3.7b).

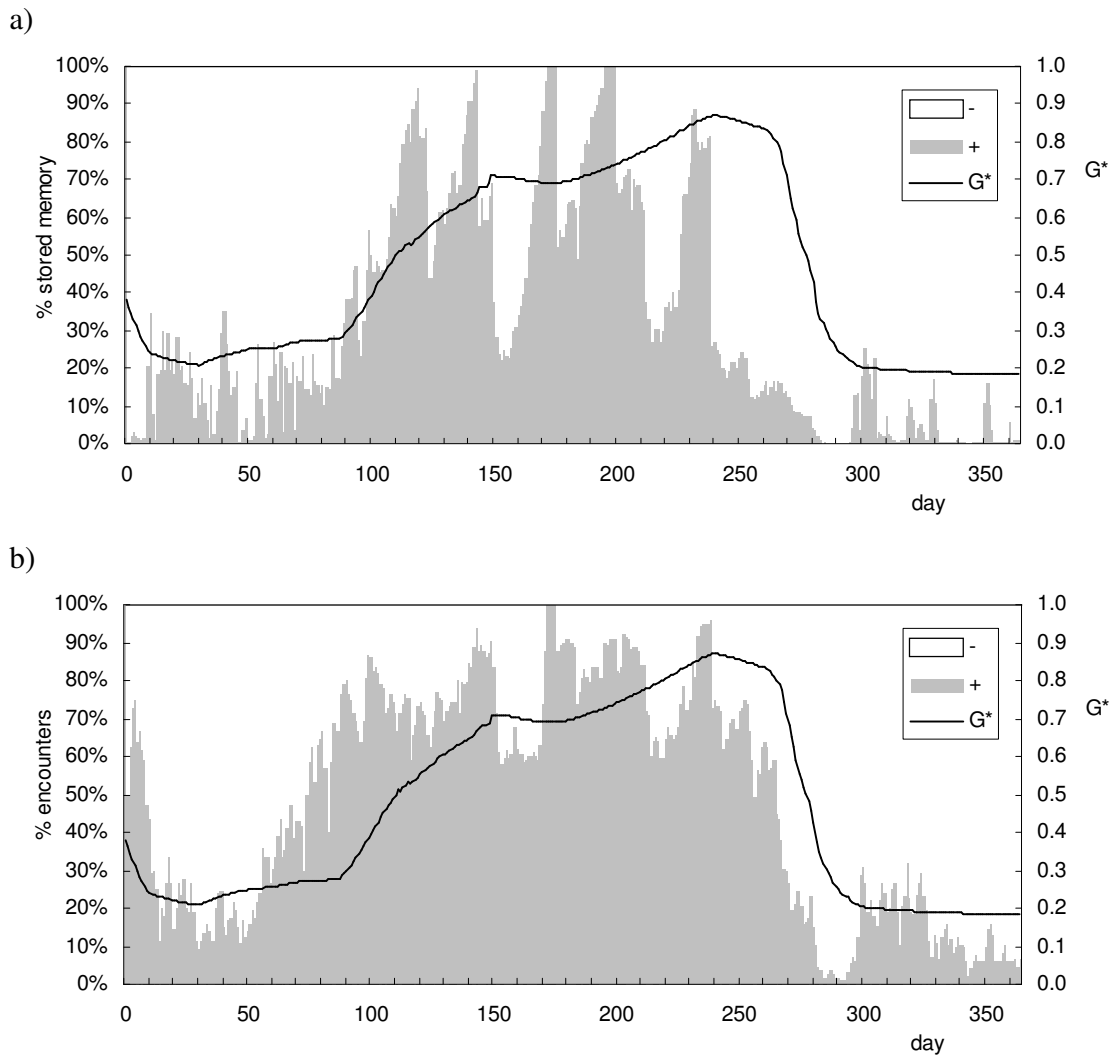


Fig. 3.7: Typical seasonal response in a) stored memory values expressed as a percentage for positive (shaded) and negative (clear) encounters in comparison with the environmental mean, G^* (line), and b) the percentage of the number of those encounters giving rise to those memorized values. For a grid dominated by negative memories, animals are repelled from their latest locations towards less recently visited areas. This occurs mainly during the dry season. When resources are more abundant, for most of the wet season, animals are attracted back to recently visited sites.

Encounters were remembered for each cell (co-ordinates ij). Memory values (M_{ij} , $J s^{-1}$) from simulation of foraging on the current day were not used for assessment until the following day, and the means for each directional segment (see Section 3.13.7) were used to avoid bias from non-central herd positions.