

Spatial behaviour of grazing livestock and the memory of food position

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Summary

This paper reviews the major factors determining the distribution of grazing animals in farmed and rangeland systems. The effects of vegetation type, water, topography and social factors are discussed. The final section examines the capacity of grazing animals to remember the position of food sources and argues that the association between food quality and spatial cues is a separate entity distinct from the association between specific sensory cues and individual foods.

Recent data on learning suggest that long-term memory of food cues requires short-term exposure over a number of days but information on spatial cue learning is not available. These observations suggest that training of animals to a combination of 'mobile' spatial and feed cues could increase the rate of acceptance of new feeds by grazing animals.

Introduction

The acquisition of food can be seen as a series of 'decisions' within the territory or home range of grazing animals. The animals must first make a choice about the areas or plant communities where they will be located on a regular basis and within these areas they will then make decisions about the patches (an area of 5–100 m²) where they will spend most of their time when feeding.

Once the patches have been identified the next decision to be made is 'which feeding station (position of feeding without moving feet) will be sampled next?' The process of recognition or testing of the diversity and availability of feeds at a feeding station will involve the senses of smell and touch and, once a bite has been taken, taste. The decision to continue eating will be influenced by social factors and also by familiarity with the feeds and alternative choices, while spatial decisions about the next patch chosen will be influenced by memory of previous feeding events.

Figure 1 illustrates the various levels of decision making for grazing animals seeking food and highlights some of the factors that will modulate these decisions. The role of memory 'loops' is also illustrated to highlight

the importance of memory of feed position and feed characteristics to later food choices. However we will examine more closely those factors modulating spatial position before we look in detail at the role of memory in spatial decisions relating to feeding.

Plant communities and home range

Herbivores are able to travel quite long distances in search of food and can utilise food sources that fluctuate widely in both quantity and quality. However, there is a wide variety of factors influencing the distance that grazing animals will travel to obtain food. Geographical location including vegetation type and quality, soils, slope and weather conditions all influence their distribution. Grazing animal distribution tends to be irregular over the land area available because it results from the integration of those factors and their influence on social, feeding and environmental needs.

The concepts of territory and home range are widely used in behavioural studies to describe the areas routinely defended or frequented by animals. Home range areas have been identified for groups of cattle by a number of workers. Kil and Boroski (1996) identified a home range area for cattle of between 160 and 280 hectares in a region dominated by shrubs and with little grass under-story. The cattle preferred to graze in riparian areas or areas cleared as a result of burning. Forbs in the riparian zone and grasses in more elevated areas were the preferred plant species eaten. Howery *et al.* (1996) also reported home range and habitat use in a herd of 116 cows observed regularly over a 2-year period on Idaho rangelands; four home range areas were identified for the herd with 78% of cows showing consistent usage in, and 33% complete fidelity for, an area. A similar pattern was also identified in the context of watering points for cattle herds in central Australia (Hodder and Low 1978). The groups of cattle in the four home range areas studied by Howery and his colleagues differed in the degree of foraging in riparian and upland habitats and the authors suggested that the animals

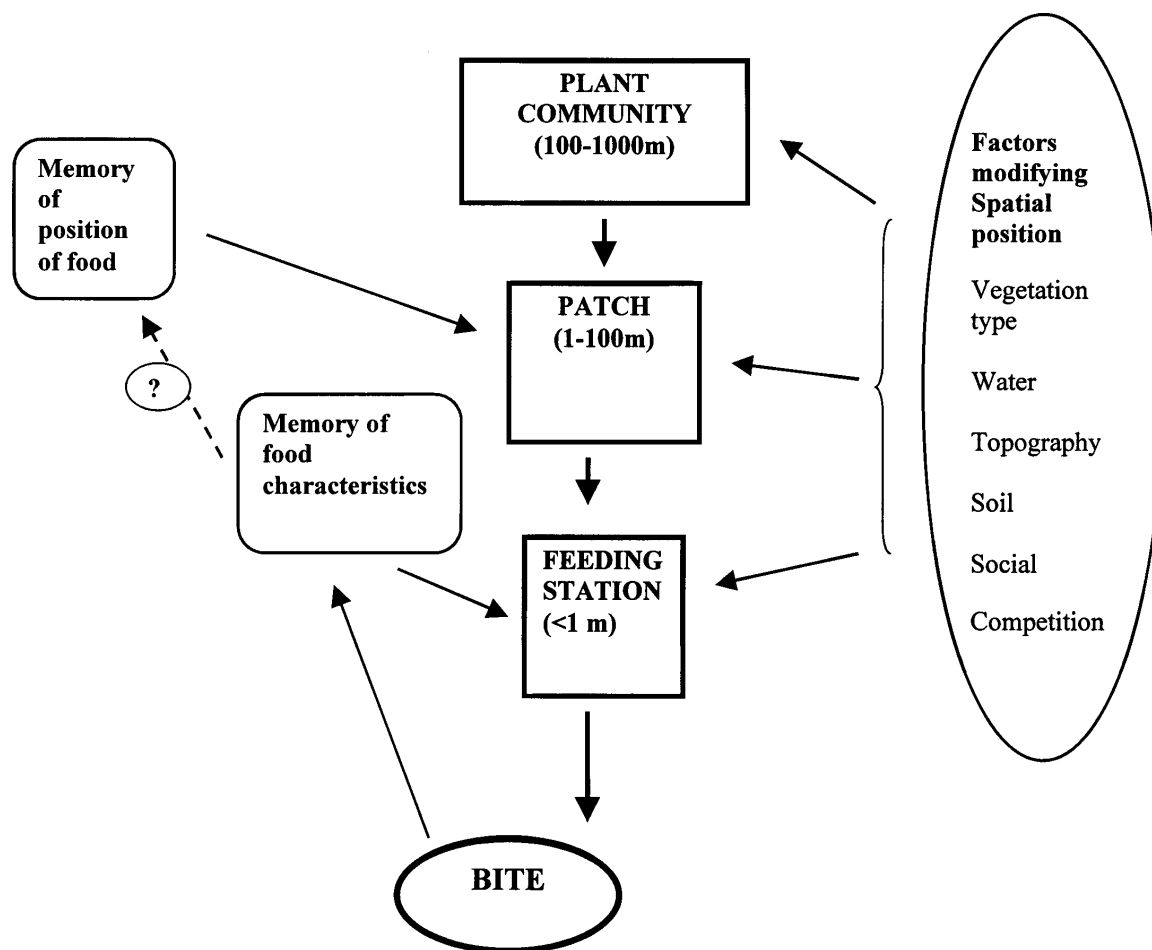


Figure 1 The factors influencing the spatial behaviour of the grazing ruminant.

had acquired these preferences when reared in different environments.

Rough terrain appears to facilitate the establishment of home range groups in cattle (Roath and Krueger 1982) and group structure is possibly based on gregariousness rather than associations between individual animals, a pattern also suggested for sheep (Lawrence and Wood-Gush 1988).

Within home range areas, choice of grazing areas appeared to be random in a study of cattle grazing range lands in Colorado and Texas (Bailey *et al.* 1990). These researchers found that cattle were rarely in the same site two days in a row and that no consistent pattern of movement could be established across seasons. However when cattle are restricted spatially to a relatively small 'home range' area then movement patterns become predictable with consistent use of the same areas each day and even at the same time of day (Hinch *et al.* 1982).

A comparison of the usage of homogeneous and heterogeneous pasture areas by steers (Bailey 1995) revealed no real preferences for patches in the homogeneous area although grazing near water at around midday was consistently observed. In the area with heterogeneous vegetation cover there appeared

to be a clear preference for the higher quality feed areas and evidence that animals were more likely to return to these areas in later days. El Aich and Rittenhouse (1988) reported similar results for sheep grazing plant communities in Morocco. They found that sheep visited areas with high feed availability more frequently, but visited and sampled feed from all areas in a 50 ha paddock.

Home range areas have been described for sheep in the Scottish highlands (Lawrence and Wood-Gush 1988). These workers found that the home range size of Scottish Blackface ewes varied with season from 25 to 50 hectares. Similar areas were observed for related groups of South Cheviot ewes (Hunter and Milner 1963). In contrast, studies of Merino ewes in a semi-arid environment in Australia could find no defined home range for this breed (Lynch *et al.* 1992) with animals ranging over an area measured in square miles.

It is difficult to predict or generalise as to how large home range areas are likely to be as this seems to be influenced by a large number of variables. For example studies of both feral sheep and goats show that the formation of male and female groups in the non-breeding season affects the extent of the area occupied as do seasonal changes in food quantity and quality. In

one of the few studies of home range behaviour in goats, O'Brien (1984) reported home ranges of around 100 ha for female feral goats in Australia rangelands. Males had an extended range of around 150 ha and the area for both groups included grassland vegetation grazed primarily in summer and also heath/shrub land that was the primary winter food source.

Factors influencing the choice of plant community/patch utilised

Vegetation and water

The distribution of grazing animals often correlates well with vegetation type, the most preferred plant groupings including willows and shrubs, sedges, and moisture-loving grasslands commonly referred to as the riparian zone. These plants provide green feed and moisture at times when it is not available elsewhere. Such effects are particularly apparent in arid areas of Australia used by both sheep and cattle (Muller *et al.* 1976).

Low *et al.* (1981), using aerial survey techniques to identify the major factors influencing distribution of Shorthorn cattle in central Australia (190 km² survey area), found that both quality and quantity of vegetation influenced cattle distribution with disruptions caused by sporadic rainfall, dry watering points and cold winds. The cattle appeared to prefer woodland areas dominated by *Aristida* and *Enneapogon* grass spp. or flood plains grass species. In drought conditions the cattle utilised the less preferred areas and plant species. Pickup and Bastin (1997), using similar techniques but evaluating changes in vegetation cover, confirmed the effects of vegetation type on cattle distribution and also emphasised the effect of the availability of water and the distance which animals would travel.

The distribution of animals is influenced by the location of water, and species and breeds differ both in their tolerance of water deprivation and also the distances they are willing to travel between food sources and water. These differences are a major determinant of the distribution of animals in drier rangelands. For example, sheep forced to walk to water reduced grazing time on the day of walking (El Aich *et al.* 1991) but compensated by increasing grazing time the following day. Sheep have been reported to travel for distances of up to 25 km per day in rangeland conditions and for as little as 5 km where pasture availability is high. Much of the distance travelled in rangelands may not be directly associated with food gathering but rather to movement between preferred 'patches' where water is located.

Sheep breeds may differ in the distance they travel and Bown (1971) reported that Rambouillet ewes travelled further than Columbia ewes and that all breeds travelled further in the morning than afternoon, the greater distance being associated with the sheep walking considerable distances to water. The morning grazing period was significantly shorter (4.5 hours) than

the afternoon (5.5 hours). The early grazing period appeared to occur predominantly in 'preferred feeding areas' and not near water. In contrast to this, in a more temperate environment, Lawrence and Wood-Gush (1988) reported major use of the riparian zone in the late morning and early afternoon when animals were less likely to be feeding and 'more likely to seek water'.

Cattle have been observed to drink in the late afternoon, the amount consumed varying with climate, physiological state and diet. Again the location of cattle is to a degree influenced by the distance to water sources but rangeland studies reveal that cattle will travel large distances to water before returning to preferred grazing areas. Alternatively the areas close to natural-water sources may be overgrazed.

Topography

The steepness and length of slope is known to influence the distribution of grazing animals and the consequent utilisation of forage. Possibly the best documented evidence for this is the study of Mueggler (1965). He found that cattle foraged (in terms of utilisation of bunchgrass) closer to the foot of a slope as the slope became steeper. However the common presence of water and riparian areas at the base of slopes possibly confounds this observation.

Slope aspect has been reported to be of importance in cold climates with animals preferring the sunny face and often not utilising the shaded face possibly due to lower temperature and reduced feed availability. Sheep and cattle often establish overnight camp areas that are usually in upper slope positions normally facing the early sun (Taylor and Hedges 1984). Sheep prefer to camp on hilltops near to their grazing areas and McDaniel and Tiedmann (1981) noted that sheep favoured ridges for grazing and camping but were willing to utilise slopes of up to 40° for grazing. In a detailed analysis of factors influencing distribution they identified slope, percent bare ground and soil surface characteristics as more important than vegetation variables, at least on hilly country. In a similar study with cattle Cook (1966) ranked slope, slope adjacent to water and distance to water as the most important variables influencing distribution on mountain range in Utah.

There are clear differences between grazing species in their response to slope. For example on Utah summer range, deer were observed to spend the majority of their time on slopes of 30–40% while cattle utilized slopes of less than 10% (Heady and Child 1994). Sheep and goat distributions appear to be less influenced by slope than is cattle distribution.

Soil type (correlated to some degree with slope) may also play a role in animal distribution as home range areas have been linked to soil type and associated vegetation cover; however, this is a circular argument and it seems almost impossible to determine which is the more important. The interrelationships between these variables make them interdependent in the context of many field studies of food choice. For instance deer

have been reported to browse the same plant species to different degrees depending on the soil type on which the plants were growing. Were these differences due to soil nutrient differences causing changes in plant nutrient content or to different stages of maturity of the plants?

Launchbaugh *et al.* (1990) found no significant differences in the proportions of forage chosen by cattle on sandy or clay loam soils when foliage was abundant but noted that as availability declined so selectivity was reduced, and diets more closely matched the existing plant proportions in each soil area. A number of studies have reported effects of soil fertility and/or fertiliser application on choice of grazing areas. For example Cootes and de Feuvre (1998) reported a study conducted in the dry tropics of Australia where there was an increased preference for *Stylosanthes* spp. fertilised with phosphate fertilizer although this preference was not always consistent. Similar effects have been observed for grazing steers (Jones and Betteridge 1994).

The availability of salt within an environment may also be a factor that influences distribution. A number of studies of wild and feral ungulates have reported the 'attraction' of salty areas to animals (Carbyu 1975). Heady and Child (1994) have suggested that where sources of dissolved salts are not readily available, cattle distribution can be altered by the strategic placement of salt.

Social issues

Social factors are extremely important determinants of many of the behaviours of gregarious species and as such could be predicted to have a large impact on the feeding behaviour of grazing animals. The effect of flock associations/bonds on animal distribution and social facilitation of feeding has been reviewed for sheep by Lynch *et al.* (1992). Such factors may also interact with group size and the home range areas required for these groups.

It seems likely that, to some degree, spatial distribution and therefore selection of plant communities is influenced by the bond between mother and young or between age groups. Likewise the formation of bachelor herds and the impact of sexual behaviours is also likely to influence spatial distributions. This is likely to be reflected in the transfer of feeding/spatial information via traditions of the maternal line where associations are potentially maintained for a number of generations. For cattle, social links appear to be based more on a dominance hierarchy than associations although in a natural setting the links of animals with maternal groups is strong and, like sheep, the transfer of information about feeding areas by maternal traditions is possible.

Association between species is also a possibility, and when lambs were reared with cattle Anderson *et al.* (1990) showed that the sheep did not influence cattle diets. However, the 'bonded' sheep increased intake of

grass (7%) and ate fewer forbs and shrubs (9%) compared to the non-bonded animals thus mimicking more closely the diet of the cattle. This difference, although relatively small, suggests that the food choices of sheep may be influenced by cattle possibly by changes in spatial distribution, the sheep selecting foods from the 'patches' in which the cattle are located.

Scott *et al.* (1996) reported the effect of familiarity with the environment on the ability of sheep to learn about feeds. They suggested that social factors are more important than previous food experiences/ preferences if animals are in a novel environment. However if most sheep in a group are strangers (socially unstable group) then memory of preferred food locations may become a major determinant of foraging location rather than maintenance of social contact (Scott *et al.* 1995).

Clearly there is a link between social factors, spatial location and food sources. Further studies are needed to determine which is cause and which is effect. Further studies are also needed to determine if animals are more likely to venture into spatially unfamiliar areas and/or unfamiliar food patches if they are in socially stable groups.

Memory for a food or for a location?

A number of studies have attempted to evaluate the capacity of animals to remember the position of foods/ food sources. While these studies have been restricted to relatively small areas they all suggest that a degree of accuracy in spatial memory exist for sheep, cattle, goats and deer. In a series of rather complex experiments Edwards *et al.* (1994, 1996, 1997) were able to show that sheep retained the ability to identify preferred food positions (in an arena of about 400 m²) using a combination of spatial memory, searching and sampling behaviours. Visual cues associated with the foods hastened the correct spatial choices, and after a short learning period animals normally moved directly to the patches containing the higher quality food. Similarly Laca (1998) demonstrated that young crossbred steers were able to return to locations where small quantities of a high quality pelleted food had previously been found. He also showed that the steers systematically searched for food if the position of the pellets was not consistently in the previous position.

If we assume that spatial memory capacity of animals is limited then the accuracy of long-term memory for location is likely to decline with an increase in the number of sites to be remembered (Laca 1998). Therefore long-term memory is more likely to be used to locate persistent resources such as water, shelter and feeding areas rather than for location of specific plants/foods whose position will change with changes in pasture conditions.

Hosoi *et al.* (1995a,b) have used maze tests to explore the capacity of sheep and goats to respond to

short term changes. In these studies it was apparent that goats, and to a lesser extent sheep, established a pattern of moving first to the position where the high quality food was previously found but rapidly shifted to a new position if the expected food quality was not high. Bailey *et al.* (1989) also demonstrated the existence of short-term memory for feeding sites between grazing bouts for cattle.

A synthesis of these findings suggests that grazing animals may associate a position cue with a food source but that searching behaviour is a means of compensating for inaccuracies in finding the correct position. Certainly the use of spatial memory allows animals to achieve greater intakes of 'good quality' food and a higher 'foraging efficiency' as measured by feed eaten per distance walked at least at within patches.

If these findings on memory are correct, and can be generalised to larger areas, then the position of grazing animals is likely to be determined by long-term (reference) memory of spatial cues which identify the location of resources such as high quality food, water and shelter. However, anecdotal observations of the responses of cattle and sheep to the cue of a vehicle used to transport feed supplements would suggest that an association between 'mobile' visual and auditory cues and a high quality food source is also rapidly acquired. Thus 'reference' memory cannot be limited to permanent cues but may include a variety of visual cues not necessarily with permanent spatial links.

The previous discussion about spatial memory for food resources suggests that increasing food quality/availability (possibly linked with ease of harvesting as well as nutritional quality) is a major factor determining

the development of an association between food source and spatial cues. What we don't know is whether the information recorded about specific foods/cues is integrated with the spatial information or if they are independent events. We do know that farm animals rapidly learn to associate specific food cues (most often texture, odour or taste) with aversive post-ingestive effects (Provenza *et al.* 1994) but evidence for associations between food cues and positive post-ingestive effects is more difficult to find (Nolan and Hinch 1997). In neither case is there evidence to suggest that animals specifically link these food-cue associations with spatial information. Therefore there is the possibility that the 'memory circuits' which record associations between specific foods and cues and those circuits linking food quality/resource availability with spatial cues are separate (Figure 2). If this is true then the animals must utilise memory of spatial cues and their association with food quality/availability to locate the patch containing a rich food source. Once positioned in the appropriate patch, they will search this patch utilising memory of the cues specifically associated with aversive or positive post-ingestive or sensory feedback, to locate acceptable foods and update information about specific foods or cues.

Associations between foods and cues

The large variability in the acceptance of new foods (particularly supplements) by grazing animals (Nolan and Hinch 1997) has been largely attributed to a

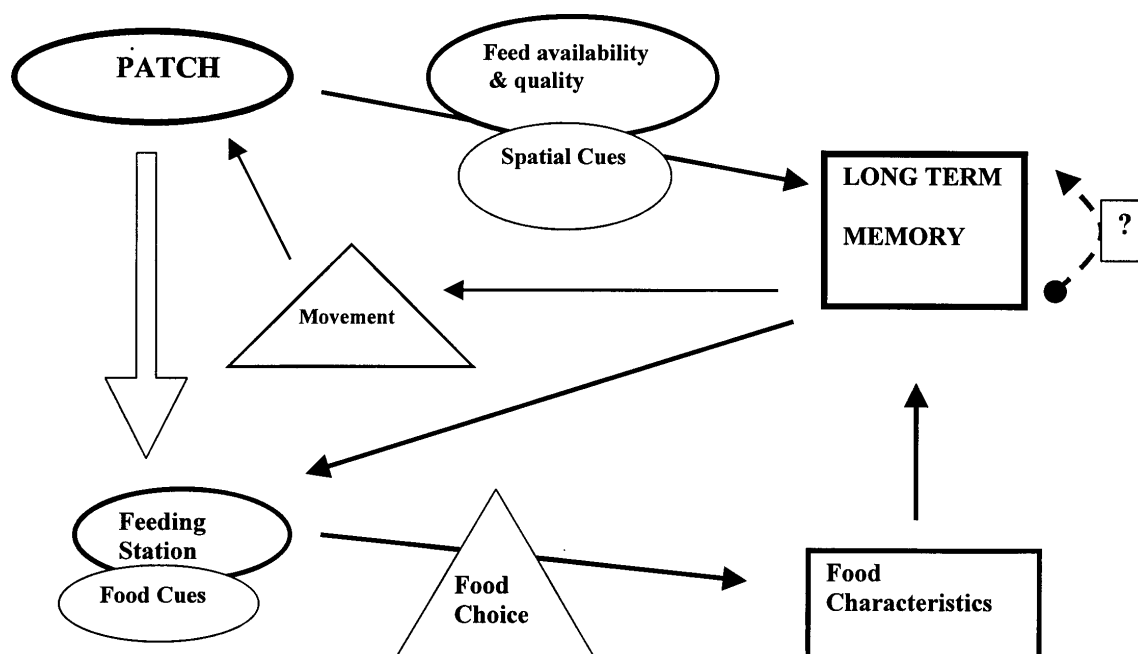


Figure 2 The interrelationships between memory for spatial cues associated with patch recognition and specific food cues associated with food choice.

neophobic response of grazing animals to unfamiliar foods and potentially to the surroundings of that food (Chapple and Lynch 1986). Recent studies with sheep at the UNE have examined in greater detail the process of learning about new foods. We have been able to hasten by a number of days the rate of acceptance of new foods by using familiar plant cues—utilising memory for familiar plant odour or flavour cues previously associated with positive post-ingestive or taste outcomes (Tien *et al.* 1999). Figure 3 illustrates the learning curves associated with establishment of such food acceptance and it appears that if the food cues are unfamiliar then neophobia for the food is overcome only by the repeated exposure of animals to these cues.

In a study using young Merino weaners we were able to show that sheep exposed every second day, every day or twice daily to a new food all took the same number of days of 5 minute exposures to a new food before they commenced eating significant quantities (Figure 4). Total time and frequency of exposure to the food were not important determinants of the learning curve; this suggests that short-term exposures to food cues over a number of days is needed to establish memory of the association between new cues and post-ingestive consequences of the new food.

At present we have no clear evidence whether this pattern of learning is similar for the links between spatial

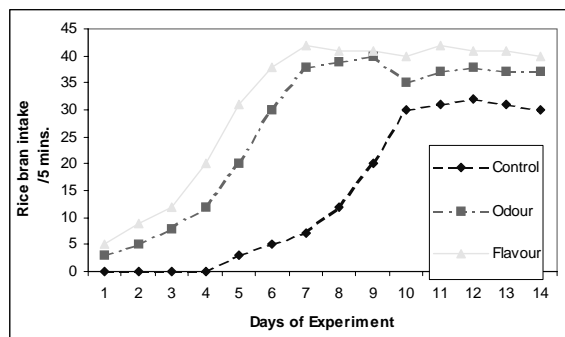


Figure 3 The learning curve of weaner sheep exposed, for five minutes per day, to a novel food, a novel food with familiar odour, and a novel food with a familiar flavour.

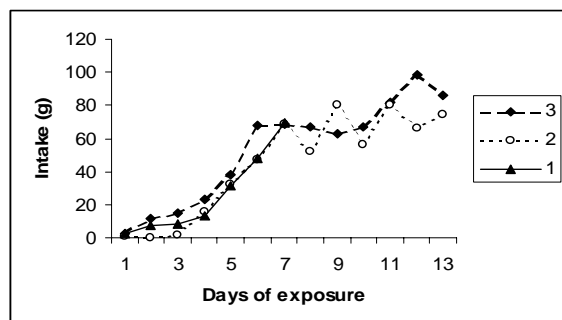


Figure 4 The intake of a novel feed (lupins) by sheep exposed to this feed for five minutes: 1, every second day; 2, once every day; 3, twice a day.

cues and resource availability. Anecdotal information would suggest that a learning/conditioning process over a number of days is necessary to establish recognition of links between spatial cues and food resources, but experiments are necessary to confirm this.

In conclusion it would seem that spatial memory plays an important role in the location of animals within an area of plentiful food resources. Animals appear to establish an association between visual or auditory cues relatively quickly and these appear to be retained in long-term memory. This memory circuit appears to be different from that used to record associations between cues and food post-ingestive consequences and both forms of memory need to be considered in the development of management systems that will encourage ready acceptance of new feed supplements by grazing animals. At present experimental evidence suggests that training animals about new foods should involve the use of an animal's memory of familiar spatial and food cues. This is possibly most easily achieved by conditioning of animals to 'mobile' visual cues and food odour or taste cues in early life. Subsequently these cues can be linked to any new feeds that need to be given. This combination should ensure that all animals are located within the appropriate feeding patch and that they recognise the food as familiar and therefore acceptable.

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