# CHAPTER 2A

# MECHANISMS DETERMINING
# LARGE-HERBIVORE DISTRIBUTION

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**Abstract.** Grazing distribution is an important component of the foraging ecology of large herbivores. Recognising the differences in foraging behaviours that occur along spatial and temporal scales is critical for understanding the mechanisms that result in grazing distribution patterns. Abiotic factors such as topography, water availability and weather and biotic factors such as forage quantity and quality affect the distribution of large herbivores. Numerous empirical studies have shown that large herbivores typically match the time spent in an area with the quantity and quality of forage found there. Although the observed grazing patterns have been documented, the underlying behavioural processes are still being elucidated. Cognitive foraging mechanisms assume that animals can use spatial memory to remember the levels of forage resources in various locations, while non-cognitive mechanisms require that behaviours such as intake rate, movement rate and turning frequency vary in response to forage resource levels. The ability of animals to use spatial memory during foraging has been demonstrated in several species including livestock, which suggests cognitive mechanisms are possible. Optimal-foraging theory can also be used to help explain behavioural processes. Giving-up rules based on marginal-value theorem appear to work well for large herbivores when a patch or feeding site can be noticeably depleted within an appropriate temporal scale such as a grazing bout or when forage availability is limited. However, giving-up rules do not always explain movements among feeding sites when forage is plentiful. The satiety hypothesis has been used to explain the avoidance of toxins and the acquisition of nutrients in diet selection. We suggest the satiety hypothesis can be expanded to account better for the variability in feeding-site selection. Large herbivocres should move among feeding sites when forage availability becomes limiting or when animals become satiated. Satiation with feeding sites may occur because of the presence of toxins or nutrient imbalances or because of aversive external stimuli. Large herbivores may return to sites that were previously considered aversive due to a combination of individual animal variation and social factors. Large herbivores can now be readily tracked using global positioning system (GPS) technology, which will allow us to test predictions of the satiety and other hypotheses and to better understand behavioural processes associated with foraging.

**Keywords.** diet selection; feeding site; giving up; grazing; patch selection; satiety

## INTRODUCTION

Movement patterns of animals during foraging are a critical component of their behavioural repertoire that affects total energy expenditures, exposure to variable thermal conditions, predation, and availability of food items (Stephens and Krebs 1986; Moen et al. 1997; Yearsley et al. 2002). The distribution of individuals reflects their movement patterns and can therefore be studied to gain insight into the behavioural mechanisms that result in these distribution patterns. The distribution patterns of large herbivores have been well studied and empirical approaches such as multiple-regression models have been used to predict grazing patterns (e.g., Low et al. 1981; Allen et al. 1984; Senft et al. 1985a; Brock and Owensby 2000). However, these models are often site-specific (Senft 1989), and in the case of multiple-regression approaches, they are not spatially explicit and do not address the underlying behavioural mechanisms (Coughenour 1991; Bailey et al. 1996). Since large herbivores have a large impact on their resources, the distribution of grazing across the landscape is also critical for maintaining the productivity and biodiversity of rangelands and pastures (Vavra and Ganskopp 1998; Holechek et al. 2001), which is why land managers have been working on methods to increase uniformity of grazing on heterogeneous rangeland for over 45 years (Williams 1954; Savory 1988; Gordon et al. 1990; Bailey 2004).

*Behavioural mechanisms determine large-herbivore foraging patterns at intermediate scales (food patches and feeding sites)*

Behavioural mechanisms that result in grazing distribution patterns vary at different spatial and temporal scales, but there appear to be some commonalities among the mechanisms (Bailey et al. 1996; Senft et al. 1987a). These scales can be distinguished by the temporal intervals between behaviours and by the spatial dimensions of the choices (Kotliar and Wiens 1990).

At coarser scales, abiotic factors such as topography, distance to water and temperature often act as constraints within which biotic factors such as forage quantity and quality operate (Senft et al. 1987a; Bailey et al. 1996; Duncan and Gordon 1999). In response to climatic conditions, wild herbivores may move up or down elevation zones to take advantage of the variability in plant phenology. Migrations from one region to another may result from lack of forage or water or changes in precipitation patterns (Senft et al. 1987a). Many species migrate or disperse, which allows them to survive in spite of the variability in weather and climatic patterns (see Boone et al., Chapter 9).

Biotic factors such as forage quantity, nutrient and toxin concentrations affect grazing behaviour at fine and coarse scales. Herbivores select food items that are abundant and that are high in nutrients and low in toxins (Baumont et al. 2000; Provenza et al. 2003). Herbivores also select patches and feeding sites where forage is more abundant, nutrients are more concentrated and toxins are at lower levels (Senft et al. 1985a; Scott et al. 1995; Coppedge and Shaw 1998).

The objective of this chapter is to review some behavioural mechanisms that may be important in determining large-herbivore grazing patterns at intermediate scales (food patches and feeding sites) and to discuss new insights about these mechanisms suggested by recent research. Related mechanisms that result in smaller-scale behaviours such as diet selection (see Laca, Chapter 5 and Fryxell, Chapter 6) and larger-scale behaviours such as migration and transhumance (see Boone et al., Chapter 9) are covered in other chapters.

Many of the studies used to develop and evaluate the proposed behavioural mechanisms were conducted with domesticated livestock. We rely on these studies to describe the mechanisms and often attempt to apply the concepts to other large herbivores including wild ungulates. Our focus on livestock is intentional, and is a result of our interest in wild herbivores, not a lack thereof (Box 2.1). We contend that the behavioural mechanisms and principles developed from experimental studies of livestock may have great value in explaining the foraging behaviours of wild large herbivores.

## SPATIAL AND TEMPORAL SCALES FOR UNDERSTANDING FORAGING MECHANISMS

The six spatial scales described by Bailey et al. (1996) are functionally defined and relate to foraging decisions that occur at distinct temporal scales (Table 2.1). The scales vary from a bite that occurs every 1 or 2 seconds to home ranges that change much less frequently (1 month to 2 years), if they do at all. A grazing bout is a



*Behavioural mechanisms resulting in distribution patterns vary at different spatial and temporal scales; commonalities among mechanisms exist*

period of concentrated grazing typically lasting 1 to 4 hours with large herbivores, which is preceded and followed by non-grazing behaviours such as resting and ruminating (Vallentine 2001). Multiple patches can be selected within a bout, while feeding sites reflect a coarser spatial scale and encompass the entire area grazed within a bout. Herbivore decisions that occur at even coarser scales such as daily, seasonal and lifetime ranges occur much less frequently and often are not relevant to domestic livestock in intensive grazing systems. In this chapter, we target movements and behaviours that occur temporally within and especially between grazing bouts (hours and days). We focus on the spatial selection of patches and feeding sites.

## ABIOTIC FACTORS INFLUENCE FORAGING PATTERNS

Abiotic factors influencing foraging patterns include slope, distance to water, distance to shade or thermal cover, temperature, wind, fences, barriers, and attractants such as salt or supplement (Bailey et al. 1996). Livestock generally prefer to graze gentle terrain (Mueggler 1965). For example, Gillen et al. (1984) reported cattle avoided grazing in areas with slopes greater than 20%. Areas far from water often receive less use (Valentine 1947). Vertical distance may be more important

than horizontal distance from water in mountainous terrain (Roath and Krueger 1982). In the Himalayas, free-roaming livestock use higher elevations as the summer progresses because water availability is usually limited to snowmelt (Mishra et al. 2001; Mishra et al. 2003).

**Table 2.1.** *Temporal and spatial scales useful for describing and evaluating foraging behaviour of large herbivores (adapted from Bailey et al. 1996; Owen-Smith 2002a). Spatial levels reflect units that large herbivores may select among*

| Spatial level | Spatial resolution of selected unit[1] | Temporal interval between decisions | Defining behaviours or characteristics | Response variable | Vegetation entity |
|---|---|---|---|---|---|
| Bite | $0.0001 - 0.01 \ m^2$ | 1 – 2 s | Jaw, tongue and neck movements | Bite size | Plant part |
| Feeding station | $0.1 - 1 \ m^2$ | 2 s – 2 min | Front-feet placement | Bite rate | Plant (grass tuft, shrub) |
| Food patch | $1 \ m^2 - 1$ ha | 1 – 30 min | Animal reorientation to a new location. A break in the foraging sequence | Feeding duration | Clump of plants |
| Feeding site | 1 – 10 ha | 1 – 4 h | Grazing bout | Foraging movements | Plant species association |
| Daily range | 10 – 100 ha | 12 – 24 h | Area where animals drink and rest between grazing bouts | Daily time allocation | Landscape unit |
| Seasonal range | 100 – 1000 ha | 3 – 12 months | Migration | Metabolic allocation | Landscape type |
| Lifetime range | > 1000 ha | Several years | Dispersal or migration | Life history schedule | Geographical region |

[1] The spatial resolution of each level will vary among species of large herbivores. These approximate ranges are given to help the reader visualise differences between levels. The temporal intervals between decisions and animal behaviour are used to define the units of selection.

During cold or hot weather herbivores may select areas with more favourable conditions (see Owen-Smith, Chapter 8). During cold and windy weather, animals often seek areas protected from the wind (Houseal and Olson 1995), but cold weather may have little effect on small-scale movements if they can maintain thermoneutral conditions (Duncan et al. 2001). Preferences for certain elevations and aspects may be partially explained by thermoregulation (Harris et al. 2002). Higher elevations are often warmer than lower areas at night. Cows often prefer ridges and avoid valleys at night when temperatures are cooler (Harris et al. 2002). Conversely, during hot weather, animals seek shade (McIlvain and Shoop 1971).

*Abiotic factors influencing foraging patterns include slope, distance to water, shade or thermal cover, temperature, wind, fences, barriers and attractants*

Preferred sites for non-foraging activities such as resting, ruminating and watering are usually influenced by abiotic factors (Senft et al. 1985b; Bailey 2004). In addition to natural barriers such as cliffs, grazing can be constrained by snow depth (Johnson et al. 2001; Mishra et al. 2003), and domestic livestock are often constrained by fences. In arid and semi-arid areas, sources of water and shade are often limited, which also affects selection of feeding sites. After watering and resting, animals must decide where to begin the next grazing bout. Distances (horizontal and vertical) and routes to feeding sites are determined by the availability and location of water and shade. Attractants such as salt or supplement can modify grazing patterns (Bailey and Welling 1999), as herbivores travel to the attractant and then graze nearby areas later (Bailey et al. 2001c).

## BIOTIC FACTORS ASSOCIATED WITH FORAGE RESOURCE AFFECT GRAZING PATTERNS

Forage quality and quantity affect herbivore distribution. The amount of time large herbivores spend in a plant community is proportional to the quality and quantity of forage available (Senft 1989). Senft et al. (1987a) referred to these patterns of grazing observed at landscape scales as 'matching'. Animals match the time spent in a plant community or feeding site with the level of resources found there. Numerous studies have shown that different species of large herbivores spend more time in areas of the landscape or pasture that are more productive and have higher levels of forage quantity and/or quality, and they spend less time in areas with less food (Hunter 1962; Coppock et al. 1983; Duncan 1983; Taylor 1984; Owens et al. 1991).

Though most studies have shown forage availability and quality influence grazing patterns and habitat selection, other currencies have been used to explain and predict where large herbivores will graze. Some studies have found the abundance of certain forage species can explain selection of patches or feeding sites (Marell et al. 2002; Fortin et al. 2003). With snow cover, forage abundance and accessibility may be more important than nutrient concentration (Johnson et al.

**Box 2.1.** *Use of livestock for studying behavioural mechanisms of large herbivores*

Any discussion of large herbivores should consider livestock, given their importance and abundance throughout the world. FAO (2003) estimates there are roughly 1.4 billion cattle, 1 billion sheep and 0.6 billion goats in the world today. Similarities among domestic and wild large herbivores suggest that behavioural processes observed in domestic species may be applicable to wild species and vice versa. Wild herbivores and livestock have similar rumen or hind-gut (cecal) fermentation digestive systems (Van Soest 1982). Some wild ungulates are closely related to livestock species. For example, North-American bison can mate with cattle and the resultant offspring are fertile (Burditt et al. 2000). Social behaviour of similar-sized domestic and wild herbivores is often similar. In feral conditions, cattle can form highly stable social groups that are similar to wild bovine species such as African buffalo (Reinhardt and Reinhardt 1981; Lazo 1994; Prins 1996).

In studies of rats and ducks, researchers identified some differences in behaviour between domesticated animals and their wild counterparts (Boice 1972; Desforges and Wood Gush 1976; Price 1978). Such studies suggest that the frequency and intensity of behaviour patterns, not the kinds of behaviours, are affected by domestication (Boice 1972; Price 1984). In a study comparing domestic pigs to wild boar hybrids (Gustafsson et al. 1999), domestic pigs used a slightly less costly foraging strategy. Both domestic and wild boar hybrids responded to patch depletion and spent shorter times in a patch on successive visits.

An additional argument for the similarity of domestic and wild large herbivores is the disproportionate contribution of a single order of mammals, the *Artiodactyla*, to successful domestic animals (Stricklin 2001). Large social groups, promiscuous sexual behaviour and adaptability to a wide range of environmental conditions may have contributed to the domestication of large-herbivore species.

Scientific studies of foraging behaviour are often conducted with livestock because of their availability, docility and the ease of manipulating initial conditions for an experiment. Ancestry of livestock can often be determined (e.g., pedigrees). Using techniques such as artificial insemination and embryo transfer, the genotype and rearing conditions of experimental animals can be manipulated. For example, researchers of Montana State University are currently comparing foraging behaviour of offspring from cows that spend much more time grazing high rugged terrain (hill climbers) with that of cows that spend much more time on gentle slopes near water (bottom dwellers). To control for the genetic effects of the male parent, all offspring were sired by the same bull using artificial insemination. By using embryo transfer, all offspring were placed in unrelated cows eight days after conception. Previous grazing patterns of the recipient cows (foster mothers) were established prior to embryo transfer. The result is a 2 x 2 experimental design where the effects of genotype (hill climber and bottom dweller donor cows, 'biological mothers') and early environment (learning early in life from hill climber and bottom dweller recipient cows, 'foster mother') can be quantitatively compared. Such manipulations are virtually impossible with wild species. Thus, we attempt to understand the behavioural mechanisms of foraging from experiments with livestock. The applicability of these proposed behavioural mechanisms to wild species must be evaluated using correlative approaches.

2001). Other researchers have found large herbivores choose areas based on forage quality rather than quantity (Wallis de Vries and Schippers 1994; Coppedge and Shaw 1998; Biondini et al. 1999). Some studies have used indices that combine attributes of forage quantity and quality, such as standing N (kg N/ha), to determine where animals will graze (Senft et al. 1985a; Pinchak et al. 1991). In any case, areas that contain more high-quality forages are often preferred by large herbivores, and their preference is illustrated by the attractiveness of areas that have been burned or fertilised (Hooper et al. 1969; Ball et al. 2000).

Other biotic factors can reduce the attractiveness of forages, patches and feeding sites. Recent work with post-ingestive feedback has shown that animals dynamically select various food items to match nutrient needs and to avoid over-ingesting toxins

(Provenza 1995). The effect of these processes on the selection of patches and feeding sites is an interesting area for further research (Duncan and Gordon 1999). For instance, Scott et al. (1995) found that food preferences affected where a lamb ate, and lambs did not forage in locations of foods to which they were averted.

Human disturbance and predation can affect grazing patterns of wild herbivores. Human settlement and cover affect selection of feeding sites by European roe deer (Mysterud et al. 1999). Predators can also influence feeding-site selection (Brown 1999). Caribou may sacrifice high-quality forage to avoid areas where the risk of predation is high (Ferguson et al. 1988). In Yellowstone National Park, the increase in preferred browse species in meadows after the reintroduction of wolves suggests that elk are avoiding these open areas because of the higher predation risk (Ripple and Betschta 2003).

*Animals dynamically select various food items to match nutrient needs and to avoid over-ingesting toxins*

Conversely, an analysis of tracking data of woodland caribou suggested that predation had little effect of movements within large patches and feeding sites (Johnson et al. 2002a, 2002b). Prins (1996) argues that African buffalo ignore the risk of predation when determining where to forage, especially when living as part of a herd.

## BEHAVIOURAL PROCESSES CAUSE OBSERVED FORAGING PATTERNS

As discussed previously, large herbivores spend more time in nutrient-rich than in nutrient-poor areas of the landscape. Although this aggregate 'matching pattern' is well defined, its causes (mechanisms) are still being studied (Bailey et al. 1996). We must understand the behavioural mechanisms (Box 2.2) that result in grazing patterns before we can efficiently manage habitat and manipulate grazing patterns. In what follows, alternative behavioural mechanisms are presented and evaluated based on recent research.

### Non-cognitive foraging mechanisms

Bailey et al. (1996) proposed several behavioural mechanisms that could explain observed patterns of matching without invoking cognitive processes. For example, intake rate may vary in response to available forage. If patches become sufficiently depleted so that intake rate drops, animals will leave the patch (Jiang and Hudson 1993). This mechanism is similar to the predictions of the marginal-value theorem for patch residence time (Charnov 1976), where animals should leave a patch when the instantaneous intake rate drops to the average intake in the available habitat. However, short-term intake rate is usually controlled by bite size and is not always related to forage biomass (Gross et al. 1993a, 1993b). In situations where forage is abundant, intake is probably constrained by digestive processes, but if forage quantity is limited, intake may be constrained by the cropping process (Wilmshurst et al. 1999a).

If animals travelled slower in nutrient-rich patches and faster in nutrient-poor patches, they would correspondingly match the time spent in patches with the associated resource level. Rate of travel in some large-herbivore species may vary in different habitat types. For example, foraging velocities of goats increased with a greater abundance of inedible shrubs. However, white-tailed deer increased foraging velocity when the abundance of highly palatable browse increased (Etzenhouser et al. 1998). Goats and deer appeared to use different strategies. Goats moved more quickly in nutrient-poor than nutrient-rich patches, while deer moved faster in nutrient-rich patches because they could harvest the preferred shrubs more efficiently. Although this mechanism at first appears parsimonious, variation in travel rate is not necessarily a valid explanation of time spent in different patches. It is open to circularity.

*Foraging mechanisms can explain grazing patterns without assuming large herbivores possess cognitive abilities*

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**Box 2.2.** *Affective and cognitive processes in foraging*

Animals process information about foods and foraging sites through two interrelated systems: affective (non-cognitive) and cognitive (Garcia 1989). Taste plays a prominent role in both systems. The affective system integrates the taste of food with post-ingestive feedback (Provenza 1995). This system causes changes in the intake of food items that depend on whether the post-ingestive feedback is positive or aversive. The net result is incentive modification. On the other hand, the cognitive system integrates the odour and sight of food with its taste. Animals use the senses of smell and sight to differentiate among foods, and to select or avoid foods whose post-ingestive feedback is either positive or aversive. The net result is behaviour modification. Cognitive experiences can be further divided to include use of the senses of sight and smell to learn from mother, learn from conspecifics, and learn through trial and error about foods and foraging sites. Together, affective and cognitive processes provide flexibility for animals to maintain homeostasis as their nutritional needs and environmental conditions change.

The anatomical and physiological mechanisms underlying affective and cognitive systems have been fairly well established (Provenza 1995). Taste afferents converge with visceral afferents in the solitary nucleus of the brain stem. Taste and visceral afferents proceed to the limbic system, where hypothalamus and related structures maintain homeostasis in the internal environment through the endocrine system, the autonomic nervous system, and the neural system concerned with motivation and drive (i.e., incentive modification). Higher cortical centres interact with the hypothalamus through the limbic system, and regulate the internal environment primarily by indirect action on the external environment (i.e., behaviour modification). These alternative means of regulating the internal environment generally function in parallel. For example, the taste of food is adjusted according to the effect of those foods on the internal environment; on this basis, animals use thalamic and cortical mechanisms to select foods and foraging sites that are beneficial and avoid those that are not.

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Animals could remain in nutrient-rich areas longer by turning more frequently than in nutrient-poor areas (Bailey et al. 1996). Differences in the tortuousity in movement patterns may occur among species. Observed foraging paths of white-tailed deer were straighter than those of goats in the same landscape in Texas (Etzenhouser *et al.* 1998). Goats and white-tailed deer preferred different browse

species, and differences in spatial arrangement of species apparently resulted in differences in tortuousness of foraging paths. In a Montana study, cattle movements during morning grazing bouts were generally linear (Bailey et al. 2004), which suggests that this mechanism is not appropriate for cattle.

Changes in observed foraging velocities and turning frequencies within a patch or feeding site are likely the result of localised differences in availability and arrangement of forage. Fortin (2003) found that bison used area-concentrated searches to locate high-quality patches under the snow. Bison apparently used short-term sampling to avoid digging through snow in areas of low profitability. If forage was abundant, snow craters were congregated, and if forage was sparse the distance between snow craters was greater. Animals also use visual cues to locate food patches (Howery et al. 2000). This ability allows herbivores to move directly to the nearest patch if it is distinguishable (Gross et al. 1995).

*Cognitive foraging mechanisms*

Using radial-arm mazes, spatial memory has been demonstrated in rats, pigeons and cattle (Olton 1978; Roberts and Van Veldhuizen 1985; Bailey et al. 1989a). Maze studies demonstrate that these animals can learn the locations of food sources and avoid locations that have been depleted. Cattle can remember the quantity and quality of the food at various sites (Bailey et al. 1989b; Bailey and Sims 1998), which enables them to forage more efficiently in arena studies (Edwards et al. 1996; Dumont and Petit 1998; Laca 1998). Anecdotal observations suggest that large herbivores remember the locations of important features of their environment, such as water, shade and thermal or hiding cover. It is likely that all large herbivores have accurate spatial memories and use cognitive processes during foraging.

Bailey (1995) found cattle returned to areas of higher forage quality or quantity more frequently and returned to areas with lower quality or quantity less frequently. Over time, these behaviours should result in typically observed patterns of foraging-



*Some foraging mechanisms assume that large herbivores have cognitive abilities*

site selection where animals match the time spent at various sites with the availability of nutrients found there. Initially animals travel to nutrient-rich feeding sites to graze. Later, as nutrient-rich sites become depleted, animals may shift to other areas of lower forage quality or quantity. In an unpublished GPS (global positioning system) collar-tracking study from the Montana laboratory, cows grazing foothill rangeland followed this type of feeding-site selection pattern. Initially, cows used lower elevations near water where forage quantity and quality were higher. Later, cows used steeper slopes, higher elevations and areas further from water as the more nutrient-rich sites near riparian areas and coulee bottoms became depleted (Bailey and VanWagoner 2004).

## MARGINAL-VALUE THEOREM AND BEHAVIOURAL FORAGING MECHANISMS

The marginal-value theorem (Charnov 1976) has been used successfully for explaining patch use in optimal-foraging theory (Stephens and Krebs 1986). The patch model is based on a net energy gain function that varies with time spent in a patch. The primary prediction of the patch model is that foragers should move to another patch when the instantaneous intake rate in any patch drops to the average rate of the entire habitat. The original solution to the problem of allocating time spent in various patches implicitly assumed foragers knew how much time to spend in each patch (McNair 1982). A more reasonable assumption is that foragers compare the current intake rate with intake rates obtained in the past. The time spent in a patch would then depend on a rule-of-thumb decision concerning when to give up and leave a patch (Krebs et al. 1974; McNair 1982). For large herbivores, giving-up rules could explain why animals move as feeding sites become depleted. The standing crop of forage may be reduced sufficiently that short-term (theoretically instantaneous) intake rate decreases, and the animal would then move. Prins (1996) observed that dense herds of African buffalo readily shift from one feeding site to another and on average revisit feeding sites once every 4 to 5 days. In this study, feeding sites were 4 to 50 ha in size and were heavily grazed by buffalo and other competing herbivores. With herds of hundreds of buffalo, the quantity of forage could be reduced within hours and short-term intake rate would decline.

*Marginal-value theorem of optimal-foraging theory can explain foraging patterns when resources are limited*

At the finer scale of patch selection, the marginal-value theorem and giving-up rules should work even better than at the coarser scale of the feeding site. Large herbivores, especially groups and herds, could noticeably deplete a patch (1 m$^2$ to 1 ha) within a period of minutes to hours. Wapiti moved to another patch when biting rate began to decline, which is in agreement with the marginal-value theorem (Jiang and Hudson 1993). The time wapiti spent in a patch was usually less than 6 minutes, thus the temporal and correspondingly spatial scale in this study was much finer than feeding-site selection. The marginal-value theorem also successfully predicted patch selection of cattle with patch sizes of 0.6 m$^2$ (Laca et al. 1993).

These studies suggest that giving-up rules based on optimal-foraging theory work well for large herbivores when a patch or feeding site can be noticeably depleted within an appropriate temporal scale such as a grazing bout or when forage availability is limited. However, at least for cattle, and perhaps for other large herbivores (Box 2.3), giving-up rules based on the marginal-value theorem do not appear to work well for explaining movements among feeding sites when resources are plentiful or when grazing in an area has recently begun and forage is not limiting. In such cases, animals typically under-match – they over-use poorer sites and under-use richer sites (Kennedy and Gray 1993). Wapiti, for example, alternate between high- and lower-quality patches and spend more time foraging in patches of lower quality than predicted by optimality models (Wilmshurst et al. 1995). In

gentle terrain with relatively homogeneous vegetation, cattle rarely graze in the same section of a pasture for more than 2 consecutive days (Bailey et al. 1990; Bailey 1995). It is unlikely that changes in forage availability explain this alternation among feeding sites, as less than 5% of the available forage was harvested before cattle switched feeding sites. With GPS technology, researchers can readily observe feeding-site selection. When a 337-ha foothill pasture in Montana was divided into 9 zones based on topographical features, cattle did not graze in the same zone for more than 3 consecutive days (Bailey unpublished data). Indeed, the cows often moved to a zone on the opposite side of the pasture.
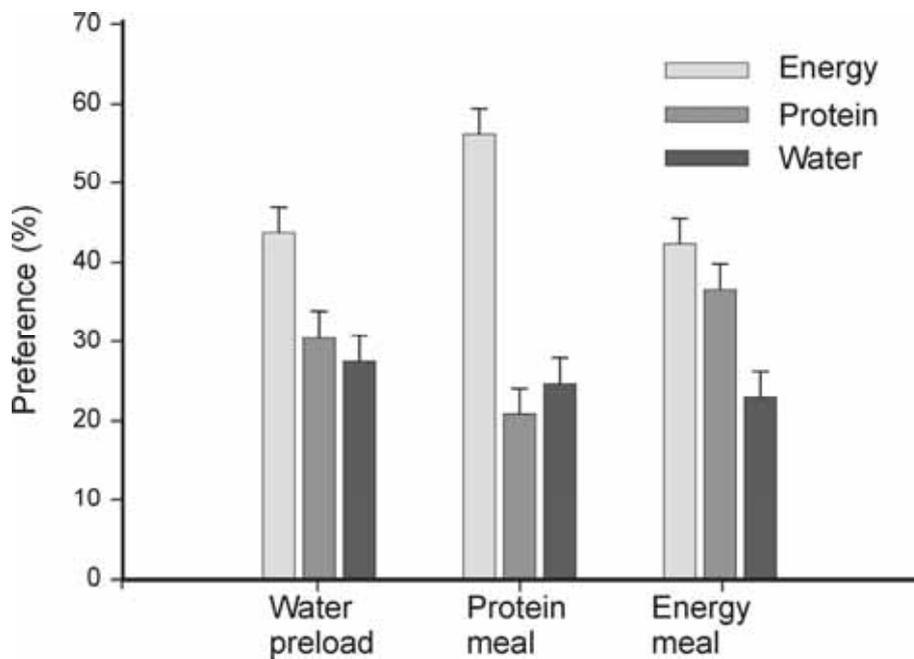


**Figure 2.1.** Nutrient-specific satiety. In the study of Villalba and Provenza (1999), lambs were given flavoured straw followed by oral gavage of energy, protein or water; a different flavour was paired with the different nutrient sources during conditioning. Following conditioning, lambs were given a pre-load meal of either water, energy or protein, and offered a choice among straw in the three flavours. Lambs preferred energy > protein = water when fed a basal diet of alfalfa pellets high in protein. When offered straw in the three flavours immediately after a meal high in protein, lambs strongly preferred energy > water > protein. Conversely, when offered straw in the three flavours immediately after a preload of energy, lambs preferred energy = protein > water. Note the strong degree to which preferences for energy and protein changed as the trials progressed from water to protein to energy.

Why do cattle and other large herbivores alternate among feeding sites when preferred forage is still abundant where they are foraging? Bailey et al. (1996) developed a conceptual model to explain alternation in feeding sites with similar resources. This model relied on memory decay to explain why animals return to areas they previously avoided. However, recent studies with diet selection and anecdotal observations suggest that an animal's memory of aversive events remains for long periods (Provenza 1995, 1996). Conceptual models used to explain diet selection and acquired food aversions of large herbivores may also be applicable for understanding movement patterns.

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**Box 2.3.** *Nutrient-specific satieties*

Animals learn to discriminate among foods based on feedback from nutrients (Provenza 1995, 1996). Energy- or protein-deficient sheep learn to prefer poorly nutritious foods such as straw when their intake is accompanied by intraruminal infusions of energy (Villalba and Provenza 1996; 1997a; 1997c) or protein (Villalba and Provenza 1997b), both of which can condition strong food preferences. Sheep maintain ratios of energy to protein that meet nutritional needs (Egan 1980; Provenza et al. 1996; Wang and Provenza 1996) by discriminating between feedback from energy and protein following food ingestion (Villalba and Provenza 1999, Figure 2.1).
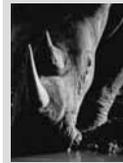
Preferences for foods high in protein or energy are governed by the nutritional state of insects (Simpson and Raubenheimer 1993, 1999), rodents (Gibson and Booth 1986, 1989; Perez et al. 1996; Ramirez 1997; Gietzen 2000; Sclafani 2000), and ruminants (Cooper et al. 1993; Kyriazakis and Oldham 1993, 1997; Kyriazakis et al. 1994; Berteaux et al. 1998; Villalba and Provenza 1999). Animals prefer a food high in energy after a meal high in protein and vice-versa (Figure 2.1). Elk optimise macronutrient intake by selecting appropriate patches of grass, though there has been debate over whether energy (Wilmshurst et al. 1995) or protein (Langvatn and Hanley 1993) is more important (see Fryxell et al., Chapter 6). Modelling efforts and experimental analyses show that both are critical, and that the preferred ratio of protein to energy depends on needs for growth, gestation and lactation (Wilmshurst and Fryxell 1995; Fisher 1997; Villalba and Provenza 1999).

The synchrony of nutrient fermentation also affects food intake, which increases with appropriate ratios of energy and protein and decreases with an excess of either (Kyriazakis and Oldham 1997; Villalba and Provenza 1997b; Early and Provenza 1998). The balance of energy and protein affects the rates of production of end products of microbial fermentation such as organic acids and ammonia. The rate at which energy and protein are released cannot exceed the rate at which they can be processed without causing excesses of organic acids or ammonia and decreases in intake. Hence, rates of fermentation of energy and protein influence intake (Cooper et al. 1995; Francis 2002).

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## SATIETY HYPOTHESIS IN DIET SELECTION

Ruminants eat an array of plant species, varying in nutrients and toxins. This selection makes intuitive sense, but no theories adequately explain this diversity. Some maintain that this variety in diet selection reduces the likelihood of overingesting toxins (Freeland and Janzen 1974), whereas others contend it meets nutritional needs (Westoby 1978). Nevertheless, herbivores seek variety even when toxins are not a concern and nutritional needs are met. The satiety hypothesis provides an explanation that encompasses both the avoidance of toxins and the acquisition of nutrients (Provenza 1995, 1996).

A key concept in the satiety hypothesis is aversion, the decrease in preference for food just eaten. Aversions are due to interactions between sensory (taste, odour, texture – i.e., flavour) and post-ingestive (effects of nutrients and toxins on chemo-, osmo-, and distension-receptors) effects unique to each food. Flavours result when



*Satiety hypothesis may explain variability in diet selection*

sensory receptors in the mouth and nose respond to gustatory (sweet, salty, sour, bitter), olfactory (an array of odours), and tactile (astringency, pain) stimuli. These receptors interact with visceral receptors that respond to nutrients and toxins (chemo-receptors), osmolality (osmo-receptors), and distension (mechano-receptors). Collectively, these neurally-mediated flavour-feedback interactions enable animals to discriminate among foods, each of which possesses a distinct utility, and they encourage animals to eat a variety of foods and to forage in a variety of locations (Pfister et al. 1997; Early and Provenza 1998; Villalba and Provenza 1999; Scott and Provenza 1998, 2000; Atwood et al. 2001a, 2001b).

The satiety hypothesis makes three testable predictions. First, the hypothesis attributes varied diets to transient food aversions due to flavours, nutrients and toxins interacting along concentration gradients (Provenza 1995, 1996; Provenza et al. 2003). Gustatory, olfactory and visual neurons stop responding to the taste, odour and sight of a particular food eaten to satiety, yet they continue to respond to other foods (Critchley and Rolls 1996). Second, aversions should become pronounced when foods contain too high levels of toxins or nutrients or nutrient imbalances. Aversions also result when foods are deficient in nutrients or when amounts of nutrients required for detoxification are inadequate. Aversions occur even when a food is nutritionally adequate because satiety and surfeit are on a continuum. Finally, cyclic patterns of intake of different foods are due to eating any food too often or in too large an amount (Provenza 1995, 1996), and the less adequate a food is relative to an animal's needs, the greater and more persistent the aversion (Early and Provenza 1998; Atwood et al. 2001a, 2001b).

The satiety hypothesis helps to explain why sheep prefer to eat clover in the morning and grass in the afternoon, even though clover is more nutritious than grass (Newman et al. 1992; Parsons et al. 1994). Hungry sheep initially prefer clover because it is more digestible than grass. As they continue to eat clover, however, sheep acquire a mild aversion likely from the aversive effects of byproducts of nutrient fermentation – excess organic acids produced from soluble carbohydrates and ammonia produced from highly digestible proteins (Cooper et al. 1995; Francis 2002) – and from the aversive effects of cyanogenic glycosides (Burritt and Provenza 2000). The mild aversion causes them to eat grass, which is relatively lower in nutrients and toxins than clover, in the afternoon. During the afternoon and evening, the aversion subsides as sheep recuperate from eating clover. By morning, they are ready for more clover.

While most explanations for varied diets stress why animals seek other more nutritious alternatives, they do not account for why animals stop eating highly nutritious foods. Transitory food aversions explain why animals stop eating

particular foods, and flavour-feedback interactions provide a mechanism for the response. Aversions yield benefits: obtain a nutritious diet, reduce ingestion of toxic foods, optimise foraging and rumination times, sample foods and maintain a diverse microflora in the rumen. These are often mistaken as the cause of varied diets.

## SATIETY HYPOTHESIS IN FEEDING-SITE SELECTION

Though developed to explain the dynamics of diet selection, the satiety hypothesis may be useful for explaining observed shifts in feeding sites at both low and high levels of forage availability. As preferred food items become limited, large herbivores begin to eat less preferred foods. Similarly, large herbivores switch from preferred to less preferred feeding sites as forage availability becomes limited (Figure 2.2). According to the satiety hypothesis, the behavioural mechanisms for switches between feeding sites, often described in optimal-foraging theory as a 'giving-up rule' (Stephens and Krebs 1986), involve satiating on a particular food or foraging location as they become increasingly less adequate (deficient, excessive or imbalanced) relative to needs.

While the satiety hypothesis emphasises flavour-feedback interactions involving so-called gut defences, large herbivores may also switch to alternative feeding sites when forage is still abundant as a result of feedback from both gut- and skin-defence systems (Box 2.4). Feedback from the gut-defence system can cause animals to



*Satiety hypothesis can account for the dynamics of feeding-site selection*

switch to alternative sites if either a necessary nutrient is deficient or if nutrients or toxins are excessive. If available food items at a feeding site are deficient in a nutrient or cause toxicosis, animals become averse to the food/site, which causes them to switch to a site that contains the needed nutrient. Lambs challenged by an imbalance of energy or protein in their basal diet forage in areas where food items that complement their imbalance occur (Scott and Provenza 2000). Cattle trained to avoid eating a high-quality food by pairing the food with a toxin (LiCl) not only avoided eating the food, they also avoided the area where the food was first fed when it was the only food available in that area (Cibils et al. 2004).

Feedback from the skin-defence system also may affect feeding-site selection. Abiotic factors such as steep slopes, distances far from water, and cold or hot temperatures may make a feeding site adverse, whereas the opposite would cause place preferences. Cattle avoid areas where they have received electric shock (Markus et al. 1998; Cibils et al. 2004), and animals avoid areas where the risk of predation is high (Ferguson et al. 1988; Brown 1999; Ripple and Beschta 2003). The converse is true in species where risk of predation is low, for example African buffalo (Prins 1996).

In summary, there is growing evidence that animals satiate on nutrients and toxins, and this causes the dynamics of food selection as discussed above. Less is known about gut defences and feeding sites. Animals may become satiated with a

feeding site when it contains food items that result in a mild aversion due to nutrient imbalances (Villalba and Provenza 1999) or excesses of toxins (Provenza 1996). Even less is known about skin defences and locations. In general, researchers have not tested experimentally hypotheses that animals satiate on feeding sites based on gut-defence responses or on locations per se based strictly on skin-defence responses. However, the stereotypic behaviour observed in wild herbivores confined in zoos (Pollard and Littlejohn 1996; Bashaw et al. 2001) or in livestock confined in small stalls (Redbo 1992; Redbo et al. 1998) are undoubtedly examples of a satiation based on location. The apparent aversive nature of cages in zoos and small stalls in livestock operations can occur even though the diets are well balanced and varied. Providing periodic environmental change may reduce stereotypy in general (Hutchins et al. 1984; Bashaw et al. 2001).
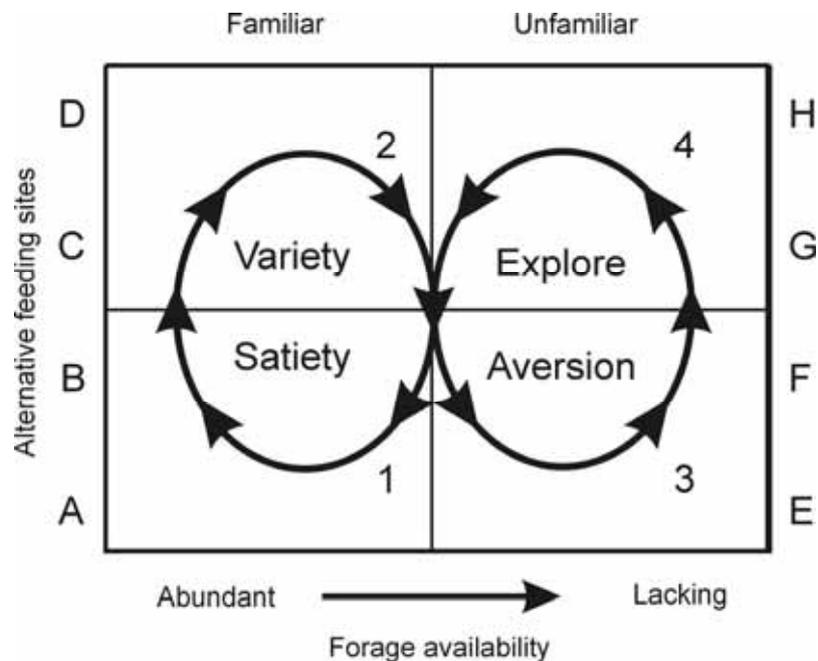


*Figure 2.2.* *Proposed dynamics of feeding-site selection behaviour based on the satiety hypothesis. When forage in the habitat or pasture is abundant, large herbivores select familiar feeding sites that are more productive and require less travel effort (quadrants 1 and 2). After one or more visits to the same feeding site, animals may become satiated to the site because of mild aversions to the foods (gut-defence system) or the location (skin-defence system) (Box 2.4). Aversions encourage animals to choose alternative feeding sites and increase the variety of sites selected. As forage levels in familiar and more desirable feeding sites begin to decrease, animals become more likely to investigate new options (aversion – explore, quadrants 3 and 4). If environmental conditions are acceptable and the forage resources are at least comparable with current levels at previously visited sites, animals will then include them as familiar alternatives (quadrants 1 and 2).*

**Box 2.4.** *Skin and gut defences*

Animals learn about the consequences of their behaviours due to feedback from external (exteroceptive) and internal (interoceptive) environments in two fundamentally different ways. They associate what happens in specific places (exteroceptive) with positive and aversive consequences, thereby acquiring place preferences and aversions. They also associate specific foods with positive and aversive post-ingestive consequences (interoceptive), thereby acquiring food preferences and aversions. Place/food preferences and aversions are dynamic and transitory, as discussed for the satiety hypothesis.

Animals learn about foods and places in different ways. As the pre-eminent psychologist John Garcia points out, "All organisms have evolved coping mechanisms for obtaining nutrients and protective mechanisms to keep from becoming nutrients" (Garcia 1989). In many birds and most mammals, auditory and visual stimuli and sensations of pain and satisfaction are associated with the so-called skin-defence system, evolved in response to predation. The taste of food and sensations of nausea and satiety are part of the so-called gut-defence system evolved in response to toxins and nutrients in foods. Odours are associated with skin- or gut-defence systems, depending on the behaviour. The odour of predators forewarns the skin-defence system, while the odour of food serves as a cue for the gut-defence system.

The way skin- and gut-defence systems work is illustrated in trials with hawks fed distinctively coloured or flavoured mice (Garcia y Robertson and Garcia 1987). When hawks normally fed white mice are given a black mouse, followed by an injection of a toxin, the hawks eat neither black nor white mice. They do not discriminate between mice as a food item based on colour. However, when a distinct taste is added to black mice, hawks learn to avoid black mice on sight after a single black-mouse toxicosis event. The hawks discriminate between food sources based on taste. These and other experiments show that not all cues are associated readily with all consequences (Garcia and Koelling 1966). Animals made ill following exposure to audiovisual and taste cues show much stronger aversions to the taste than to the audiovisual cue. In contrast, if they receive foot-shock following the same cues, they show much stronger aversions to the audiovisual than to the taste cues.

The same kind of response has been demonstrated for food and place aversions (Garcia et al. 1985). Toxins decrease palatability, but they do not necessarily cause animals to avoid the place where they ate a particular food; this is the essence of the hawk–mice toxicosis experiment. Conversely, an attack by a predator may cause animals to avoid the place where they were eating, but it does not decrease the palatability of the food. While place aversions are specific to the site, food aversions depend on the food and are generally independent of the location where the food was eaten.

Two kinds of memory underlie both skin and gut defences. Declarative (cognitive) memory is generally thought of as the process by which earlier conscious experiences are recalled (LeDoux 1992). The original learning and remembering are both conscious events. Such declarative memory is mediated by the hippocampus and the cortex. In contrast, emotional (non-cognitive) memory is mediated by the thalamus, amygdala and cortex, and in all likelihood operates independently of conscious awareness. Nevertheless, emotional information may be stored within declarative memory and retrieved in parallel, "their activities joined seamlessly in conscious experience" (LeDoux 1994). Thus, for example, acquired preferences and aversions are part of emotional memory, and in the case of specific foods, post-ingestive feedback and memory of the feedback event occur whether or not animals are conscious (Provenza et al. 1994). The emotional memory (satiating feedback from nutrients or nauseating feedback from excesses of nutrients or toxins) is stored within declarative memory of specific foods and the context in which they were eaten.

PROPOSED MECHANISMS BY THE SATIETY HYPOTHESIS

*Memory and sampling*

When forages are abundant, for example after a pasture change or during late spring while forage is growing rapidly, animals will first select preferred areas they know (Figure 2.3). Although forage is still plentiful, they may periodically change feeding sites as they satiate with characteristics (foods/location) of the site. One might expect they would first use areas that they remembered had higher levels of resources in the past. As forage in nutrient-rich or environmentally favourable feeding sites becomes depleted, animals will explore other areas of a pasture or habitat. As more feeding sites are visited, animals may become averted to some sites because of undesirable forage or environmental conditions. Animals should alternate among more novel sites with more favourable conditions along with previously preferred sites.
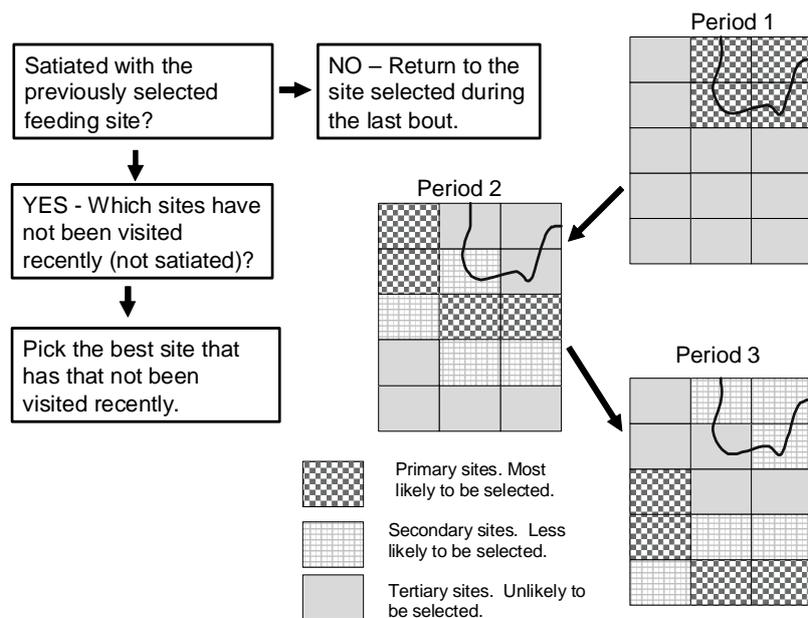


*Figure 2.3. Description of the decisions herbivores may make for selecting feeding sites based on the satiety hypothesis. If animals are not satiated with a feeding site, they will likely return to the same area. If animals are satiated, they will select another site. The pattern of changes in feeding-site selections is presented. Initially (period 1), animals alternate among the best feeding sites near the stream. As the animals become satiated with the streamside sites, they select sites further from water (period 2) (stream given by black line). As animals become satiated with those sites, they will select sites even further from water (period 3) and may return to the streamside sites, which could contain high-quality forage regrowth.*

Over time, this proposed mechanism should result in more time spent in nutrient-rich sites and less time spent in less productive sites. The alternation among sites should result in animals spending similar amounts of time in locations with similar resource availabilities. Nevertheless, animals should also sample less productive sites as they become satiated with the sites containing higher and intermediate levels of resources. This is an important prediction of the satiety hypothesis because large herbivores such as cattle periodically visit virtually all areas of a pasture or habitat. Gillen et al. (1984) found cattle sign (tracks and faecal pats) in virtually every part of a mountain pasture in Oregon, even in upland areas where forage utilization was less than 10%.

Satiation and alternation among feeding sites could have long-term benefits for large herbivores. In environments where change is the only constant, satiating on the most familiar (that visited most recently) causes animals to explore continually the less familiar (that visited in the past) and the novel (the unknown). Eating a variety of foods produces many health benefits related to nutrition, parasite loads and ingestion of compounds that in low concentrations might promote health (Engle 2002). Indeed, it is likely the most important thing an animal can do to maintain health is to eat a variety of foods that vary in concentrations of nutrients and toxins. Thus, periodic sampling of alternative foods and feeding sites may ensure an adequate food supply in rangeland environments where forage conditions can change dramatically in both time and space due to variable climatic conditions, thereby contributing to fitness.

As animals become satiated, alternative feeding sites may become more attractive. However, it is unlikely herbivores would readily revisit sites that were perceived to be very poor because of forage conditions, predation or difficulty in reaching, for example long distances from water. Animals likely remember sites that were unusually attractive or adverse for long periods. Bailey (1995) observed that steers avoided an area with lower forage quality for 21 consecutive days after first sampling the site. The satiety hypothesis predicts that the more averse the consequence, the longer the period before an animal will again engage in the behaviour.

*Variation among individual animals*

Differences among individuals in food intake and preference depend in part on variations in how animals are built morphologically and how they function physiologically, and marked differences are common even among uniform groups of animals in needs for nutrients (Scott and Provenza 1999) and abilities to cope with toxins (Provenza et al. 1992). Differences in foraging behaviour among individuals result from variability in genotype and experiences early in life (Provenza et al. 2003). Individual herbivores also have very different grazing patterns. Cattle breeds developed in mountainous terrain use rugged topography much more uniformly than breeds developed in more gentle terrain (Bailey et al. 2001b). Bailey et al. (2004) tracked cows in Montana and found that some individuals use steep, high terrain, while others prefer gentle terrain (Figure 2.4). Differences in grazing patterns
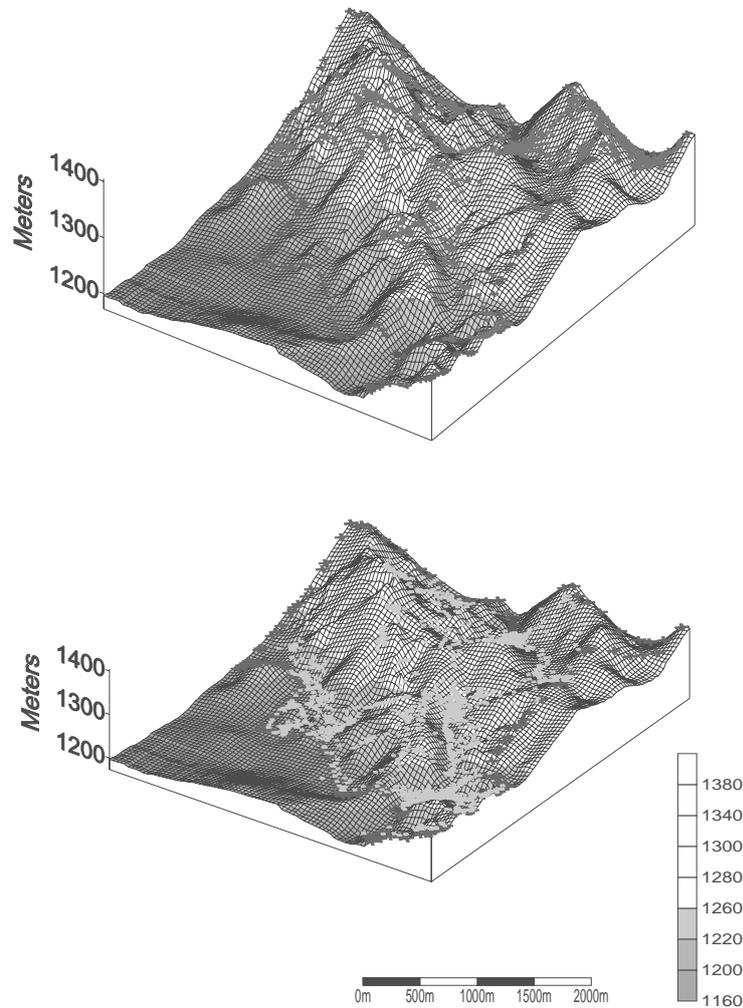
**Figure 2.4**. *Distribution patterns of two cows recorded by GPS (global positioning system) tracking collars in a 337-ha rangeland foothill pasture in northern Montana during a 3-week period in late August and early September. Cow locations were recorded every 10 minutes during the day and every 20 minutes at night. Both cows were 7 years of age and were lactating. During the previous year cow 1179 (upper figure) was observed more frequently on steep slopes and high elevations, while cow 1080 (lower figure) was observed much less frequently in these areas. These cows were purposely selected as extremes from the previous year's observations collected by observers on horseback. Cow 1080 was Hereford, a breed developed in England. Cow 1179 was Tarentaise, a breed developed in the French Alps. In addition to these 2 cows, 178 other lactating cows were grazing in the pasture during the period of observation. Water was available in streams*

observed among cattle breeds (Herbel and Nelson 1966; Bailey et al. 2001a; 2001b) suggest feeding-site selection may be at least partially heritable.

Experiences early in life affect feeding-site selection in sheep and cattle. Key and MacIver (1980) evaluated habitat selection of 2 breeds of sheep. The Welsh mountain breed that preferred native rangeland was smaller in size (36 kg), and had lower reproductive rates (90%). The Clun forest breed was larger (54 kg), had higher reproductive rates (150%), and preferred more productive seeded habitats. These researchers conducted a cross-fostering experiment where Welsh dams reared Clun lambs and Clun dams reared Welsh lambs. After weaning when lambs were 6 to 7 months of age, Welsh-reared Clun lambs preferred native rangeland, and Clun-reared Welsh lambs preferred seed habitats. Howery et al. (1996) determined that different cows grazed in different areas within extensive mountain pastures during summer and they used the same areas during the next four summers; they then studied the habitat preferences of offspring from these cows. When evaluated after weaning at 2 and 3 years of age, daughters preferred the areas that their mothers preferred. This study also included a cross-fostering experiment where female calves from cows that preferred one area of the habitat (drainage) were reared by unrelated cows (foster mothers) that preferred a different habitat (adjacent drainage). Cross-fostered offspring preferred the areas where they were reared by their foster mother. We suggest that nature (genome) and nurture (learning) interact to influence habitat selection behaviours including not only where individual animals go but also their propensity to roam (Moore 2002).

*Social influences*

When ingesting a novel food is followed by toxicosis, herbivores acquire a strong aversion to the food that can last at least 3 years. Nevertheless, the aversion will diminish if animals with the aversion observe peers consuming the food (Ralphs and Provenza 1999). A similar response may occur with selection of feeding sites.

Social interactions among herbivores influence grazing patterns (Mendl and Held 2001). In sheep and cattle, social interactions within groups encourage animals to eat a broader array of foods (Scott et al. 1995), and to forage in a greater variety of locations (Howery et al. 1998), as individuals maintain the cohesiveness of the group (Dumont and Boissy 2000) and respond to ever-changing preferences of individuals within the group. Social interactions may allow animals within the herd to transfer information about the environment as experienced animals help naïve animals find food (Bailey et al. 2000; Ksiksi and Laca 2000). Where herds of African buffalo choose to forage may be a communal decision (Prins 1996). Individuals appear to orientate toward various feeding sites, and the direction the herd takes is a result of a consensus of herd members.

SYNTHESIS

It is likely that satiation, variation in individuals within the herd, and social interactions all interact to cause alternation among similar feeding sites and periodic sampling of all sites. For example, cattle may become satiated with feeding sites near water and travel to a new feeding site further from water. If forage conditions at the new site are not as good as the conditions near water, they probably will not visit

*Forage depletion, satiation, individual variation and social interactions interact and result in alternation among feeding sites*

there again soon, especially if the longer travel distance was perceived as adverse. However, some individuals within the herd might not perceive the travel as adverse as others and visit sites further from water again. As these individuals travel to the further sites, others in the herd who had avoided the sites may now visit them with their peers. Cattle often follow individual animals with 'purposeful movement' (Greenwood and Rittenhouse 1997), and in a Montana study, cattle followed animals that walked away from the group at a faster pace in a specific direction (Bailey et al. 2000). This behaviour appeared to facilitate the transfer of knowledge of feeding locations from experienced to naive animals. Social interactions may also encourage animals to resample areas previously visited and perceived as less desirable.

Thus, the combination of forage depletion, satiation, individual variation and social interactions can result in a dynamic process where animals periodically sample locations within their home range. This periodic sampling of poor sites could be due to memory decay, as is incorporated in the cognitive foraging model proposed by Bailey et al. (1996). However, while memory decay probably occurs at some level, forage depletion, satiation, variation in individual animals, and social interaction may better account for the variability in many observed behaviours.

Recent technologies such as GPS tracking collars and geographical information software (GIS) enable researchers to evaluate movements of large herbivores at temporal scales from minutes to months. Previously, it was impractical and cost prohibitive to observe bout-to-bout or day-to-day movements of large herbivores over weeks to months. These difficulties limited the number of empirical studies of feeding-site selection of large herbivores. Much of optimal-foraging theory was developed for diet and patch selection, which could be observed during periods of minutes to hours and in laboratories and small field areas. The three hypotheses given in Box 2.5, developed from the conceptual behavioural mechanisms of feeding-site selection described in this chapter, could not have been tested 10 years ago, but they can today.

**Box 2.5.** *Testable hypotheses for future research*

*Hypothesis 1.* Abiotic factors such as slope, horizontal and vertical distance to water can increase travel effort to reach feeding sites, and in mountainous terrain these factors interact to influence use of feeding sites. For example, steep slopes may be more aversive if they are further from water (Mueggler 1965). We expect that indices that combine the effects of slope and distance to water (horizontal and vertical) will be more useful in predicting large herbivore grazing patterns than if terrain attributes are considered independently. Similarly, indices of effective temperature that combine ambient temperature and wind speed or ambient temperature and solar radiation may explain terrain use of large herbivores more accurately than climatic factors considered independently. In rugged topography, large herbivores can move and thereby modify elevation, aspect and slope to seek or avoid wind and direct sunlight. Ongoing research suggests spatially explicit models that include terrain and environmental factors can explain movement patterns of livestock and likely other large herbivores (Harris et al. 2002).

*Hypothesis 2.* Based on the satiety hypothesis, large herbivores should alternate among feeding sites not only when forage resources are sparse but when they are plentiful as well. When forage availability is limited, animals should move to an alternative feeding site as short-term intake begins to decline. When forage availability is plentiful, animals should move to alternative feeding sites without a measurable change in short-term intake rate or forage abundance due to satiating on nutrients and toxins in the forages on offer. Studies of cattle suggest that this might occur (Bailey et al. 1990; Bailey 1995; Laca et al. 1993), but more rigorous examinations with livestock and other large herbivores are needed.

*Hypothesis 3.* When forage is plentiful, large herbivores should satiate more quickly to a feeding site when the terrain and/or forage in a pasture or habitat is homogeneous than when it is heterogeneous. For example, livestock should alternate among feeding sites more frequently in pastures seeded with monocultures than in pastures with mixtures or on rangeland with mixtures of native vegetation. Large herbivores should become satiated and alternate among feeding sites more frequently in gentle terrain than in mountainous terrain. We have a limited amount of data to support this hypothesis. Cattle were tracked in two similar-sized pastures (approximately 350 ha) in Montana for 30-day periods using GPS collars. The first pasture contained rugged terrain and was grazed in late summer. This pasture was stratified into four sections based on topography and was considered more heterogeneous due to topography and the variability in forage quality typically observed in late summer. The second pasture contained more gentle terrain and was grazed during autumn. This pasture was stratified into three sections based on topography and was considered more homogeneous. Cattle in the first (heterogeneous) pasture were observed in the same section of the pasture for 4 or more consecutive days during 87% of the total days of observation. In contrast, cattle in the second (homogeneous) pasture were in the same section of the pasture for 4 or more consecutive days during only 20% of the total days of observation. Although these data support the satiety hypothesis, more extensive studies are needed with livestock and with other large herbivores under a variety of conditions designed specifically to test predictions of the satiety hypothesis.