Chapter 7
Integrating Nutrition and Animal Welfare in Extensive Systems

Juan J. Villalba, Xavier Manteca, Philip E. Vercoe, Shane K. Maloney, and Dominique Blache

Abstract Extensive systems present herbivores multiple biotic and abiotic challenges such as temporal and spatial variation in the availability and quality of food and water, changes in the chemical and morphological defenses of plants, thermal stress, disease, predation, and competition. Due to variability in resource abundance and quality, food intake might not always satisfy their appetite or hunger. Animals can adapt by increasing their grazing time and/or by dispersing more widely. These changes in behaviour may improve the use of poor quality pastures, but may also have negative effects on productivity and welfare. For instance, poor pasture conditions lead to reductions in mating activity and reproductive performance, decrease the efficiency of behavioural strategies aimed at decreasing parasitic loads, and increase energetic costs. Thermoregulation has an energetic cost, which decreases animal production. However, a lack of exposure to thermal stress may not necessarily imply adequate animal welfare. Plant secondary compounds (PSC) can inhibit food digestion, increase metabolic costs, and potentially have toxic effects on animal tissues and metabolic processes, but at appropriate concentrations certain PSC may improve nutrition and immunity and alleviate some of the diseases that challenge herbivores in extensive systems. Predators have both a direct lethal impact on herbivores and indirect effects that challenge animal nutrition and welfare. They may restrict the use of high-quality habitats and increase the time invested in vigilance, which restricts foraging time. In contrast to this, facilitative interactions among animals with contrasting foraging strategies may

---

J.J. Villalba (✉)
Department of Wildland Resources, Utah State University, 84322 Logan, UT, USA
e-mail: Juan.villalba@usu.edu

X. Manteca
School of Veterinary Science, Universitat Autònoma de Barcelona, 08193 Barcelona, Spain

P.E. Vercoe • D. Blache
UWA Institute of Agriculture (Animal Production), The University of Western Australia, Crawley 6009, WA, Australia

S.K. Maloney
School of Anatomy, Physiology, and Human Biology (M311), The University of Western Australia, Crawley 6009, WA, Australia

C.J.C. Phillips (ed.), *Nutrition and the Welfare of Farm Animals*, Animal Welfare 16, DOI 10.1007/978-3-319-27356-3_7

positively impact on nutrition and welfare. In conclusion, some relationships between the variables described in this chapter (thermoregulation, PSC, animal–animal interactions) and welfare do not always vary in a uniform direction. Many of the challenges described in this chapter stem from variability and unpredictability of the environment, which is largely a function of natural—instead of managerial—influences. The challenge of managers is to provide the conditions and flexibility in their operations to allow animals to express their behaviour to cope with these challenges in a way that production and welfare are maximised within the constraints imposed by an ever-changing environment.

7.1 Introduction

Extensive production systems can be defined as those systems in which animals have little contact with humans, including infrequent handling (Hodgson 1990). In contrast, in intensive animal production systems there is frequent interaction between animals and their managers. Herbivore species evolved to graze and browse in a variety of ecosystems, such as rangeland, grassland, and open pasture or shrubby and woody landscapes, and a variety of herbivores have been domesticated (cattle, buffalo, sheep, goats, and camels) to be used for production purposes. From the time of their domestication, herbivores have been mainly kept in extensive production systems. Today, there are about three billion animals managed in grazing systems, which use 3.4 billion hectares of land. That means 26 % of the earth's ice-free land surface is used for animal production (FAO 2009). Developing countries use slightly more of their land mass (~30 %) than developed countries (20.5 %) for animal production. In principle, the welfare of herbivores kept in extensive grazing systems should be assisted by the fact that they have evolved to make the best use of such varied herbivorous environments. However, animals are not always kept where they evolved, and the unpredictability of environmental factors, coupled with the management of livestock by humans, is not always a match to the adaptive features of livestock. Consequently, these mismatches represent welfare problems for livestock kept in extensive systems.

7.2 Why Animal Welfare Is Compromised in Extensive Livestock Production Systems

A key aspect of animal welfare is the ability of an animal to cope with its environment (Broom 1986). Within this functional approach to animal welfare, it is essential to assess whether the biological systems of an animal are functioning in a satisfactory manner in response to environmental changes (Duncan and Fraser 1997). However, welfare not only depends on whether the animal can cope but also on whether coping attempts have negative consequences for the animal. Therefore, there is no simple relationship between challenge and response because multiple biological functions can be affected by a very specific challenge, such as variability in level or quality of nutrition (Blache et al. 2011). Consequently, a multidisciplinary assessment of animal welfare that measures behaviour, the level of productivity, physiology, health, and immunity is required (Gonyou 1986; Broom 1991; McGlone 2001). These multiple aspects of animal welfare are encompassed in the framework designed for animals kept in captive environments known as the ‘Five Freedoms’ (Farm Animal Welfare Council 1993), namely: (a) Freedom from thirst, hunger, and malnutrition, (b) Freedom from discomfort, (c) Freedom from pain, injury, and disease, (d) Freedom to express normal behaviour, and (e) Freedom from fear and distress. Initially the five freedoms framework might not be seen as directly applicable to livestock raised in extensive systems. As pointed out by Turner and Dwyer (2007), extensive systems should not compromise the expression of behaviour, compromise the health of the animals, or induce mental distress, since the animal is in a ‘free range’ or ‘natural’ environment. Thus, some hold the view that livestock in extensive production systems are not under our control and therefore we do not have a duty of care (Appleby 1996). Since these species have coevolved with the landscape to be able to cope with the degree of variability of the environment, how could the welfare of extensive livestock be compromised? The answer is twofold: (1) there is a potential mismatch between the coping capacity of the animals and the variability of the environment of extensive systems because, by controlling stocking density, the type of livestock, and landscape availability, managers control the animal distribution across time and space, and (2) animals kept in the environment they have evolved in can still face challenges from extreme variability in foods, habitats, and environmental conditions that exceed their capacity to cope. The second situation needs to be considered here because, although those factors are not ‘controlled’ by the manager, they represent a welfare challenge.

In the following sections, we will give examples of challenges faced by ruminant livestock either because of natural factors or managerial decisions such as stocking density, choice of species, breed, or timing of breeding. The direct and indirect consequences of each challenge on nutrition will be treated with particular attention since this is a focus of this book. In most codes of recommendations for the welfare of animals, adequate nutrition is one of the primary requirements to be satisfied (Farm Animal Welfare Council 1993; Kyriazakis and Savory 1997). For each challenge, the advantages and limitations of the adaptive behavioural and physiological responses of grazing animals will be presented. We then analyse the impact of these challenges and adaptations on animal welfare under the framework of the aforementioned Five Freedoms. The following challenges are most common and relevant to ruminants kept in extensive conditions: variability of the quality and availability of food and water, the impact of environmental toxicology, predator and fear effects on intake, and competition with conspecifics and non-livestock herbivores.

7.3 Challenge 1: Variability in the Availability and Quality of Food and Water

To fulfil the freedom from hunger and thirst, it is essential that livestock have access to feedstuffs of adequate quality and quantity to be able to meet their nutritional requirements. In extensive livestock production systems, both the quality and quantity of food and water available can be limited either by environmental or managerial factors.

Environmental factors, such as rainfall patterns, drive forage production especially in semiarid and arid systems (Campbell et al. 2006), and food resources can be both variable and unpredictable, and as a consequence, affect grazing productivity (McAllister 2012). Similarly, forage nutritive value can be affected by water availability, fertilisation, and disease because of their impact on plant development (Van Soest et al. 1978).

To optimise production, managers can adopt stocking rate strategies to compensate for the fluctuation in forage supply induced by changing environmental conditions, such as variable rainfall. They can opt for a conservative stocking strategy by maintaining a relatively constant, and low, stocking rate, which would be unlikely to exceed the carrying capacity even during dry years. This strategy aims to avoid vegetation degradation, livestock losses, and potential decreases in animal welfare caused by overstocking in dry years (Campbell et al. 2006). Low stocking rates (i.e. low number of animals on a given amount of land over a certain period of time) typically promote an increase in plant species diversity, although very low stocking rates may reduce plant diversity as a result of competitive exclusion (Grime 1979). At low stocking rates, grazing typically leads to the formation of patches of different forage quality and quantity. In these conditions, herbivores prefer to graze patches of high nutritive quality, which are generally those corresponding to the regrowth of previously grazed areas (i.e. patch grazing; Adler et al. 2001). This recurrent pattern of grazing contributes to the spatial heterogeneity of the vegetation generally observed in plant communities grazed at low stocking rates.

Alternatively to low stocking strategies, managers may adopt high and constant stocking rates, using supplemental feed to maintain high stocking rates during dry years (Campbell et al. 2006). The supplementation needs to be managed carefully because, when stocking rate exceeds the maximum number of animals that can be supported by a certain environment (i.e. carrying capacity), the biomass availability per animal declines and preferred plants (typically the most nutritive in a community) are subjected to a competitive disadvantage relative to non-preferred plants (typically less nutritive or more toxic). The biased grazing leads to changes in plant community structure and composition (Dumont et al. 2007) impacting on both the biomass and the nutritive quality of forage available for grazing (Walker 1995). Herbivores select plant and plant parts at different levels of stocking rates (Provenza and Villalba 2006). However, high animal densities increase competition for food resources and reduce selectivity (Bailey and Brown 2011). Additionally, the prevalence of non-preferred plants species in the context of high animal densities can increase the risk of consumption of poisonous plants (Pfister et al. 2002), which is a reduction in the freedom from disease.

In addition to the compromised freedom from hunger and disease, high animal densities may also induce social stress, meaning there is a decrease in freedom from stress by increased competition for resources. The increase in social stress leads to disturbed grazing patterns that can present some serious welfare issues since the grazing pattern and intensity ultimately affect growth rates in herbivores (Blanc and Theriez 1998).

Independent of climatic conditions, stocking density is one of the most important factors affecting forage availability and quality (Edwards 1980; Allison 1985; De Villiers et al. 1994). While high stocking rates can exacerbate the effects of drought on vegetation by increasing mortality of perennial grasses, negatively impacting on soils and thus contributing to range degradation (O'Connor 1995), conservative stocking rates lead to underuse of forage in wet years which may be inefficient, particularly as environmental conditions (e.g. rainfall across seasons) become more variable. Alternative to the extreme stocking densities listed above, an opportunistic strategy is to change stocking rates to match temporally variable forage supply, aiming to secure quality and quantity forage and therefore insure an adequate level of animal welfare. A variable stocking density strategy means that higher stocking rates are adopted in wet years and reduced stocking rates in dry years. This dynamic strategy aims to match grazing pressure to the existing vegetation in both wet and dry seasons and consequently avoid production losses, and potential declines in animal welfare in dry years (Campbell et al. 2006).

Ranchers now recognise that they not only need to manage to maximise animal production but to improve vegetation abundance and plant species composition and to enhance the ecological integrity of their operations (Grissom and Steffens 2013). Under this framework, they implement adaptive management strategies with variable timing, frequency and distribution of grazing with positive economic returns and benefits to animal welfare.

7.3.1 Adaptive Responses to Low Quantity and Quality Forage

To match nutrient intake to requirements, herbivores have developed adaptive responses to decreases in the amount and/or quality of food available. These adaptive strategies include modification of feeding behaviour such as diet selection, or changes in foraging time, or modification of social behaviour such as dispersion. However, in extreme cases the adoption of feeding strategies or changes in social behaviour can negatively impact on welfare.

7.3.2 Diet Selection

The selection of a feeding station by herbivores in a heterogeneous landscape has been described as a hierarchical decision process which takes place at different levels: the regional level, landscape, plant community, down to the individual plant and its parts (Senft et al. 1987). According to optimal foraging theory, when food availability changes in space and time, herbivores will focus on the most profitable foods if resources are abundant (MacArthur and Pianka 1966; Stephens and Krebs 1986), and broaden their diet when the availability of resources declines (e.g. dry season, drought, winter) (Owen-Smith and Novellie 1982; Stephens and Krebs 1986). In terms of habitat use, the selection process may lead to an ideal free distribution of grazing pressure among habitats of different qualities (Fretwell and Lucas 1970). Thus, optimality models suggest that as long as the stocking density is adequate, animals should not experience any form of malnutrition.

Most models used in optimal foraging theory use energy or protein as the currency to be maximised. Lambs and goats fed diets low in energy and protein prefer flavoured foods associated with intra-ruminal infusions of energy (starch, propionate, acetate) and nitrogen (urea, casein, gluten), respectively (Villalba and Provenza 1996, 1997a, b, c; Duncan and Young 2002). Thus, herbivores are able to associate different internal states with the ingestion, or lack thereof, of different nutrients (Egan 1980; Kyriazakis and Oldham 1993). Despite the importance of energy and nitrogen, foraging animals usually face a choice of a variety of habitats and they possess multiple nutrient requirements. Thus, models based on just one currency (e.g. energy) are poor predictors of habitat occupancy (Wallis de Vries and Schippers 1994). Complementary nutrients like phosphorous have improved those predictions in free-ranging cattle (Wallis de Vries and Schippers 1994). Consistent with this, lambs deficient in phosphorous and calcium increase preferences for flavours and supplements which provide those minerals (Villalba et al. 2006, 2008). Thus, a decrease in the diversity of foods and/or habitats may compromise animal welfare (Manteca et al. 2008; Villalba et al. 2011; Catanese et al. 2013). The inability to satisfy requirements for energy, protein, and minerals can lead to nutritionally unbalanced intake, health problems, and stress. In an unbalanced nutritional environment, animals may stop eating because their requirements for the nutrient in highest concentration are rapidly satisfied without reaching the requirements for nutrients in lower concentrations, a phenomenon known as incidental restriction (Raubenheimer 1992). Alternatively, the animal may continue foraging in order to satisfy the requirements for nutrients in lower concentrations, inevitably leading to overconsumption of the nutrient in highest concentration, a phenomenon known as incidental augmentation (Raubenheimer 1992). Excessive nitrogen concentrations can lead to ammonia build-up in the blood resulting in loss of appetite, infertility, and even death (Lobley and Milano 1997). In addition, the augmentation in nutrient-rich and homogeneous food environments will compromise animal welfare because excess nutrients can induce aversive behaviour (Provenza 1996). Lambs exposed to flavours associated with high doses of energy or nitrogen become averse to those flavours (Villalba and Provenza 1996, 1997a, b), suggesting that excesses of nutrients can be a source of stress. The provision of multiple alternatives regarding foods and habitats is necessary to reach the appropriate proportion of required nutrients (Bailey and Provenza 2008) and allow a ruminant to adjust its food selection to minimise the discomfort generated by several signals produced during the ingestive process, i.e. the supply of metabolisable energy, crude protein, and neutral-detergent fibre (Forbes 2007; Gregorini et al. 2015). In contrast, animals that cannot express their diet preferences may experience frustration (Rutter 2010) or negative postingestive feedback (Forbes 2007; Villalba et al. 2010b) and therefore have a compromised welfare.

7.3.3 Foraging Behaviour

Herbivores can vary greatly the time they spend feeding in response to pasture availability and quality. Ruminants adapt to poor forage conditions by modifying the biting rate (number of bites per unit time), bite weight (amount of food taken per bite), and total grazing time (Holmes 1989) to obtain the necessary daily herbage intake. On short overgrazed pasture, herbivores are not able to sustain the bite volume (Charcon and Stobbs 1976) and, because of the reduction in stratum bulk density (Burlison et al. 1991), the bite weight decreases relative to its optimal level (Arriaga-Jordan and Holmes 1986). Consequently, to maintain intake, grazing ruminants have to graze for longer periods as forage conditions deteriorate (Squires 1981; Arnold 1985a; Lu 1988). On good pastures, domestic ruminants graze between 4 and 9 h/day (Houpt 1991), whereas, on poor forage conditions, grazing times of up to 14 h have been recorded (Arnold and Dudzinski 1978). This increase in grazing time, which includes an increase in total jaw movements and walking, can lead to fatigue before nutritional requirements have been fulfilled (Williamson and Payne 1978; Birrell 1991). Consequently, daily energy requirements increase because animals walk more per unit of grazing time (Osuji 1974). For example, grazing ruminants require more energy than penned ruminants: 10–50 % for sheep (Holmes 1989) and 25 and 75 % for goats (NRC 1981).

The physical characteristics of the plant can also affect grazing time. The fibrousness of feed is positively correlated with total chewing time (Boever et al. 1990). It would be difficult to consider this parameter to assess the welfare of ruminants because chewing efficiency is also affected by age (older animals chew feed less efficiently than younger ones, Gill et al. 1966), body weight (larger animals eat faster than small ones, Deswysen 1986), pregnancy (pregnant animals need more chewing time per kg of dry matter than non-pregnant ones, Campling 1966), jaw force (Hooper and Welch 1983), number of chews per unit time (Grummer et al. 1987), percentage of true chewing (Deswysen et al. 1987), and tooth surface area (Welch and Smith 1970). On the other hand, animals can adapt to the physical characteristic of the forage by developing specific foraging skills (Flores et al. 1989a; Hodgson 1990). For example, lambs used to eating a particular kind of plant were more efficient at foraging from it than unfamiliar lambs (Flores et al. 1989b, c). It has to be noted that these specialised grazing techniques may be unsuitable for other types of plant communities (Arnold and Maller 1977) and could limit the feeding behaviour of animals moved between very different plant communities.

7.3.4 Dispersion

The degree of dispersion of grazing animals is measured as a function of the distance between individuals of the same group, mean group size, and the distance between groups (Arnold 1985b). Dispersion is a strategy that enables animals to find scattered pockets of forage and to avoid competition for food. As forage conditions deteriorate, animals tend to split into increasingly smaller subgroups, and the distance between these subgroups also increases (Dudzinski et al. 1978). Inter-individual distance depends mainly on the breed. In sheep, for example, the distance between nearest neighbours is much greater in hill breeds than in Merinos (Arnold 1985b). On poor pastures, Merino sheep remain as a single flock in most circumstances (Lynch 1974), whereas many other breeds form subgroups under almost all conditions (Arnold 1985b). Similar differences in dispersion strategy between breeds have been reported in cattle (Hall and Moore 1986). In breeds with limited dispersion the ability to feed on poor pastures becomes restricted (Kilgour et al. 1975). Dispersion is an effective adaptation to changes in pasture quality and availability; however, the welfare of gregarious animals could be compromised because when forage conditions deteriorate, dispersion may conflict with their natural social behaviour. Assessing the impact of dispersion on the social structure is not simple because some breeds can balance the need for social contact with the need to disperse. Hill sheep are highly social during winter, living in large subgroups influenced in their movements by other group members. In summer, however, there is a marked decrease in gregariousness, with a considerable reduction in subgroup size and reduced frequency of cohesive grazing behaviour. The summer behaviour corresponds with the growth of dispersed patches of grass (Hunter and Milner 1963; Lawrence and Wood-Gush 1987, 1988). In addition to breed, dispersion is also affected by other factors such as previous experience (Zimmerman 1980), maternal experience (Key and MacIver 1980), location of preferred feed such as specific plant communities (El Aich and Rittenhouse 1988) or feedblocks (Lawrence and Wood-Gush 1988), shade (Fowler 1984), and water source (Squires 1981).

7.3.5 Water Intake

Ruminants can go longer without food than they can without water, so their welfare is very much dependent on the ease of access to drinkable water. In intensive or semi-intensive animal production systems, livestock are either watered daily or allowed to drink whenever they like. In contrast, under pastoral conditions, livestock access watering points and develop rigorous watering regimes that vary from every 3 days in cattle and donkeys, through 5 days in sheep and goats, to 7–15 days in camels (Nicolson 1984). However, the frequency of drinking is affected by the level of humidity and ambient temperature. For example, in the Australian arid zone, Merinos drink every day and twice a day when ambient temperature exceeds 35 °C (Dawson et al. 1975).

Within species, breeds differ in their adaptation to water restriction. For example, Boran cattle have large intakes of water and the intake is faster than other breeds. Boran bulls can drink up to 105 L in 6 min without suffering water intoxication, whereas temperate cattle can only drink at a third of this rate safely (Nicolson 1984). In sheep, when the distance between food and water is short, Merinos and Border Leicesters drank twice per day, but when the distance exceeded 3.2 km, Merinos drank once per day while Border Leicesters continued drinking twice daily until the distance reached 4.8 km (Squires and Wilson 1971).

To access water, livestock may have to spend time walking long distances between watering points and grazing grounds (Squires 1981) that reduces time available for grazing (El Aich et al. 1991). The time spent travelling back and forth to the watering point depends on (1) the animal's need for water, which itself depends on species, breed, climatic conditions, water content of the forage, and water quality, (2) the distance to travel, and (3) the walking speed. All of these factors should be taken into consideration when assessing the welfare of livestock kept in extensive systems.

7.4 Challenge 2: Variability in the Toxicological Environment

In extensive grazing systems, animals encounter a diversity of plants and many of those contain plant secondary compounds (PSC), especially if the animals are grazing native 'unimproved' pasture (Estell 2010). Plants produce secondary compounds for many reasons, mainly as a defence mechanism in response to herbivory and other environmental stressors such as disease and competition (Cowan 1999; Mazid et al. 2011). More than 200,000 chemical structures have been identified as PSC, including flavonoids, tannins, saponins, alkaloids, non-protein amino acids, cyanogenic glycosides, glucosinolates, and terpenes (Cowan 1999; Bernhoft 2010). The chemical diversity of PSC is the basis of the diversity of their actions on animal's organs and systems, as well as on animal behaviour (Durmic and Blache

2012). A specific PSC can have both detrimental and/or beneficial effects on animal welfare depending on the form and the dose ingested, the duration of ingestion, and the species exposed (Greathead 2003; Bernhoft 2010). Plant secondary compounds can severely alter nutrient utilisation, digestive function, respiratory and cardiovascular function, immune function, as well as impacting on the nervous system and reproductive capacity (Vercoe et al. 2009).

Feed intake and feed efficiency can be reduced by PSC because they influence diet selection and grazing behaviour (Provenza and Villalba 2006). Plant secondary compounds can be bitter and often deter animals from eating the plant or interfere with the digestive and fermentation process and can directly affect host secondary metabolism. However, the dose and mix of PSC are critical. Ingestion of PSC can reduce feed conversion efficiency (Stienezen et al. 1996), while small quantities of some PSC can increase it (Carulla et al. 2005). Similarly, fibre digestion can be reduced (Patra and Saxena 2009), not affected (Wang et al. 2009), or stimulated (Hart et al. 2007) by PSC. The decrease in digestibility by PSCs is associated with the inhibition of ruminal protozoa, cellulolytic bacteria, and fungi (Ferme et al. 2004; Sivakumaran et al. 2004) and a general inhibition of microbial fermentation and microbial synthesis in the rumen (Oh et al. 1967, 1968; Nagy and Tengerdy 1968; Lu and Jorgensen 1987).

In addition to these specific impacts on intake and rumen function, PSC can affect all the components of the digestive system of herbivores, inducing gastroenteritis, ruminal atony (Aslani et al. 2004), lower viscosity of intestinal content (Mahgoub et al. 2008), and liver damage (Waghorn 2008), as well as bladder lesions (Sardon et al. 2005), renal disease, and kidney failure (see Durmic and Blache 2012).

It is not only the digestive system that is impacted by PSC as pointed out in a recent review by Durmic and Blache (2012). The respiratory system can also be dramatically affected after the ingestion of PSC, leading to serious health problems such as alveolar emphysema and pulmonary necrosis and edema in sheep and cattle (Wilson et al. 1977). Similarly, with the cardiovascular system, ingestion of PSC can lead to cardiac arrhythmia, haemorrhagic syndrome and cardiac necrosis, and haemolysis. Plant secondary compounds can act as foreign molecules and induce inflammation and reduced immune cell count and activity and cause anaemia, or act as anticoagulants. Photosensitisation and irritation can be common in animals consuming plants rich in some PSC, such as saponins and furanocoumarins (Revell and Revell 2007; Bernhoft 2010). The effects of PSC on the nervous system are often detrimental and can be lethal, for example, some alkaloids, cardiac glucosides, and cyanogenetic glucosides are powerful neurotoxics (Ingebrigtsen 2010).

The reproductive capacity of both males and females is also impacted by PSC, with some dramatic consequences on production and welfare [for review see Blache et al. (2008), Durmic and Blache (2012)]. PSC can stimulate the expression of male reproductive behaviours (Patel et al. 2011) but can also decrease sperm production and quality. In females, PSC that affect fertility can be grouped into plants with contraceptive, anti-implantation, and abortifacient activity (Kumar et al. 2012).

Although PSC, as described above, have a large range of negative impacts on health, welfare, and the productivity of livestock, ruminants have acquired adaptive features that allow them to cope with the presence of many PSC in pasture because of co-evolution. More importantly, managers of extensive livestock systems can also take advantage of the beneficial impacts of PSC on bodily function to improve both the quality of animal production and animal welfare without compromising productivity.

7.4.1 Herbivores Adaptations to Cope with PSC

The adaptive features that allow herbivores to cope with PSC include behavioural and metabolic adaptations (Foley et al. 1999). The main behavioural adaptation is the capacity of herbivores to develop food aversions when ingesting PSC, because some of these compounds induce nausea (Provenza 1996). These aversions restrict the intake of toxin-containing plants, an outcome that contributes to enhanced fitness of herbivores to a particular environment. The presence of PSC such as alkaloids (e.g., *Delphinium* spp.; Pfister et al. 1997), condensed tannins (e.g. *Coleogyne ramosissima* Torr.; Provenza et al. 1990), and terpenes (e.g., *Artemisia tridentata* Nutt.; Dziba et al. 2006; *Juniperus* spp. Utsumi et al. 2009) reduced feed intake in cattle, sheep, and goats. However, not all PSC cause food aversions (Pfister et al. 2010) and delayed toxic effects can limit the ability of herbivores to form food aversions. For instance, because horses do not develop a food aversion when illness is delayed they may be at risk for long-acting toxins like the alkaloids found in *Senecio* and *Equisetum* species (Houpt et al. 1990). Plant secondary compounds can also reduce forage digestibility and increase acidic burdens in consumers with negative impacts on intake and productivity (Foley et al. 1995, 1999).

The digestive system of herbivores has metabolic adaptations aimed at the detoxification of the ingested PSC (Freeland and Janzen 1974; Illius and Jessop 1995). However, detoxification comes with a substantial metabolic cost (Thomas et al. 1988; Sorensen et al. 2005) so adequate supplies of nutrients need to be available or provided by the livestock manager (Illius and Jessop 1995). The consumption of a diversity of PSC may reduce the overall toxic effect of the mix because (1) diluted mixtures are less toxic to herbivores as each individual PSC may be detoxified by a specific pathway (Freeland and Janzen 1974), thereby eliminating a risk of saturation of detoxification mechanisms, and (2) the formation of gastrointestinal complexes often reduces the absorption and activity of single compounds. For example, tannins and saponins chelate each other in the gastrointestinal tract. It has been shown that by appropriate diet selection, mice can choose a mix of feeds containing tannins and saponins in a way that nullifies the effect of each compound (Freeland et al. 1985). Likewise, goats have a greater feed intake when they are offered shrubs containing a combination of tannins and saponins, compared to when they are offered single shrubs (Rogosic et al. 2006).

7.4.2 PSC as Medicinal Compounds for Herbivores

As pointed out at the beginning of this section, plant secondary compounds can have positive effects on some bodily functions when they are ingested in the right quantity, for the right amount of time, or in the right combination. These medicinal effects of PSC have a great potential to improve both the health and welfare of ruminants kept in extensive systems, where the provision for animal health by managers is limited.

Internal parasites are one of the greatest disease problems in grazing livestock worldwide (Min and Hart 2003; Waller 2006). Failure to control gastrointestinal nematodes typically results in poor growth rates, ill-thrift, and death (Min et al. 2004). Considerable attention has been given recently to bioactive plants that affect internal parasite populations (Jackson and Miller 2006), such as plant-derived tannins, alkaloids, terpenes, saponins, and sesquiterpene lactones (Hoskin et al. 1999; Kayser et al. 2003; Hernández-Villegas et al. 2011). Several in vitro and in vivo studies have suggested that condensed tannins can have anthelmintic effects against ruminant nematode parasites. Livestock feeding on plants with tannins, such as sulla (*Hedysarum coronarium*) (Niezen et al. 1998, 2002), sainfoin (*Onobrychis viciifolia*; Paolini et al. 2003), Sericea lespedeza (*Lespedeza cuneata*; Shaik et al. 2006), heather (*Calluna vulgaris*; Osoro et al. 2007), a number of acacia species (for instance, *Acacia cyanophylla*; Akkari et al. 2008), and lentisk (*Pistacia lentiscus*; Landau et al. 2010), have lower faecal egg counts—an indirect measurement of parasitic burden—than those eating plants of similar quality, or the same rations without tannins. These actions result from several physiological mechanisms such as a direct anthelmintic effect (Athanasiadou et al. 2001), impaired larval establishment (Brunet et al. 2008), decreased parasitic nematodes fecundity in females (Martínez-Ortiz-de-Montellano et al. 2010), and increases in the supply of by-pass protein that enhances immune responses to intestinal parasites (Niezen et al. 2002; Min and Hart 2003). Recent results suggest that parasitised sheep and goats increase preferences for antiparasitic PSC when experiencing parasitic burdens relative to non-parasitised animals (Gradé et al. 2009; Osoro et al. 2007; Martínez-Ortiz-de-Montellano et al. 2010; Villalba et al. 2010b; Juhnke et al. 2012).

In addition to the control of gut pathogen load (Patra and Saxena 2009), PSC can facilitate rumination, prevent/cure bloating (Viegi et al. 2003), reduce acidosis (Hutton et al. 2010), reduce diarrhoea and constipation (McGaw and Eloff 2008), reduce kidney stones, and treat cystitis (Viegi et al. 2003). Moreover, some PSC can increase the protection of dietary proteins and reduce microbial proteolysis, peptidolysis, deamination, and degradation to ammonia, allowing nitrogen to escape to the duodenum and improve nitrogen utilisation and production (Waghorn

2008). The energy utilisation of feed can be increased by some PSC by reducing the amount of methane that is produced during fermentation (Bodas et al. 2008; Vercoe et al. 2009).

Some PSC have antitussive, emollient, and expectorant properties that improve lung function [for review see Durmic and Blache (2012)]. In the cardiovascular system, PSC can have positive impacts through hypotensive, cardioprotective, and vascular-stabilising actions (Svendsen et al. 2010). Consumption of PSC may also modify the immune system and blood composition. Some PSC stimulate the immune system because they enhance both innate and specific immunity via modulation of receptors, enzymes, and immune molecules and have anti-inflammatory properties (Provenza and Villalba 2010). At the skin level, PSC can help wound formation, reduce skin irritation, and be used to treat some skin diseases and ectoparasites. Some PSC have structural and functional similarity with benzodiazepines and have been exploited for their calmative and anxiolytic activity in livestock (Durmic and Blache 2012). While the mechanisms of action remain largely unknown, plants containing saponins, alkaloids, and tannins have been used in ethno-veterinary practices to improve the welfare of animals during, and around the time of, parturition by reducing dystocia, improving expulsion of the placenta, and recovery from difficult parturition (Viegi et al. 2003).

Overall, as long as the types and amounts of PSC can be managed, the medicinal properties of PSC described above hold exciting opportunities for the improvement of animal health and welfare and the productivity of large numbers of ruminants grazing poor quality (high fibre and low protein) diets while reducing ecological impact.

7.5 Challenge 3: Variability in the Thermal Environment

Animals are raised in extensive grazing systems located in very different climates, from temperate pastures (e.g. New Zealand), rangelands in extreme climatic zones (Texas, Patagonia, north-west Australia), Mediterranean grasslands (Western Australia, Israel, Uruguay), and tropical lowlands [Colombia; See part 3 of Hodgson and Illius (1996)]. Consequently, ruminant livestock can be exposed to temperatures varying from -20 to $+50$ °C. Ruminant species are generally well adapted to a range of ambient conditions; hence they can, through the process of thermoregulation, maintain homeostasis and the functioning of all physiological systems, over a broad range of temperatures. Thermostasis is important because most extensively managed livestock are mammals, and mammalian biochemical systems function optimally over a limited body temperature range. The range of ambient temperatures within which an endotherm can regulate its temperature without elevating its metabolic rate or evaporative water loss is called the thermoneutral zone (IUPS Thermal Commission 2001). The range of both the thermoneutral zone (the range of environmental temperatures where the cost of thermoregulation in minimal) and the thermoregulatory zone (the range of

Table 7.1 Core temperature and thermoneutral range in different species [data from Brody (1945), Hahn (1999), Robertshaw (2004)]

Species	Core temperature mean (range) (°C)	Thermoneutral zone (°C)
Sheep	39.1 (38.3–39.9)	21 to 25[a]
Beef cow	38.3 (36.7–39.1)	−18 to 23
Dairy cow	38.6 (38.0–39.3)	−15 to 26
Goat	39.1 (38.5–39.7)	13 to 21

Source: Data from Brody (1945), Ames (1980), Hahn (1999), Robertshaw (2004)

[a] Dependent on the degree of wool cover. The lower critical temperature can vary from –3 to 31 °C according to plane of nutrition and fleece characteristics

environmental temperatures where an animal has the capacity to maintain a stable core temperature) depends on the evolutionary history of a given species or breed (Table 7.1). The values for the thermoneutral range given in Table 7.1 are not absolute, as there are phenotypic and genetic differences within and between genotypes. For instance, there are differences in heat tolerance (e.g. estimated through panting score, tympanic temperature, respiration rate) between heat-tolerant, cold-intolerant *Bos indicus* cattle and heat-intolerant, cold-tolerant *Bos Taurus* (Hansen 2004; Gaughan et al. 2009). Livestock exposure to particular environments in high or low latitudes may lead to environmental adaptations that will also modify the thermoneutral ranges as animals adapt to local environments physiologically and behaviourally (Provenza 2008).

Extreme variations in temperature can compromise the welfare and the production of ruminants if the conditions exceed the limits of the breed/species to balance heat gain with heat loss to maintain a constant body temperature. Heat gain is the sum of metabolic heat produced by all exothermic biological reactions occurring in the body, including digestion and rumen fermentation, plus any environmental heat, such as solar radiant heat or convective heat gain when ambient temperature exceeds skin temperature. Heat loss from an animal occurs via four routes: conduction, convection, radiation, and evaporation (Jessen 2001).

7.5.1 Ruminants Coping with Thermal Stress

Since breeds and species of production animals are translocated to new grazing systems, such as highly productive dairy cattle transported to the tropics, the capacity of each breed to thermoregulate can be compromised when there is a mismatch between environmental conditions (humidity, maximum, and minimum temperature) and thermoneutral zone for the species or breed. Then animals are said to be heat or cold stressed when they are in an environment that is above or below the thermoneutral zone, respectively. Being heat or cold stressed does not mean that an animal's welfare is compromised because endothermic animals (mammals and birds) have evolved physiological mechanisms and capacities that defend body temperature in the face of thermal stress. The adaptations of ruminants to temperature stresses involve physiological and behavioural mechanisms aiming at controlling the production or loss of heat.

7.5.2 Adaptive Control of Heat Production

During cold stress, when the environmental temperature is below the thermoneutral zone, an animal must increase heat production. Cold stress thus induces an appropriate increase in heat production through increased metabolic rate, including shivering. The elevated metabolic rate then requires a matching increase in energy intake if energy balance is to be maintained. However, the required increase in food intake is possible only if forage is readily available and of high digestibility, which is not always the case. For example, both parameters decrease dramatically when the ambient temperature reaches freezing (Adams et al. 1986; Adams 1987). The capacity of individuals to sustain the elevated metabolic rate required to achieve heat balance in the cold depends on other factors such as health status and energy stores. For example, significant mortality rates have been seen in sheep exposed to cold weather and deprived of shelter in the first few days after shearing (Lynch et al. 1980). Even in the absence of mortality, the maintenance requirement increases during cold stress, so there is less energy available within the animal for production or growth. Shelter during cold weather may be provided by long dry grass to sheep at low stocking rates. Nevertheless, the lower quality of the food resource will lead to increased grazing time relative to the absence of shelter (Arnold and Dudzinski 1978).

Since heat gain can be increased by environmental heat, such as solar radiant heat, animal exposed to high temperature will seek shade. For instance, cattle in hot weather actively seek shade, which may reduce the radiant heat load by at least 30 % (Blackshaw and Blackshaw 1994). Thus, the provision of trees and shrubs is an important source of shade for hot weather and can improve the welfare and productivity of ruminants during periods of low environmental temperatures as well.

During heat stress, ruminants can decrease heat production by reducing food intake and rumination time, because digestion is an exothermic process. In sheep, heat stress induces decreases in food intake, feed efficiency, and utilisation, a disturbance of enzymatic reactions, hormonal secretions, and blood metabolites, all of which modify water, protein, energy, and mineral balances (Marai et al. 2007).

7.5.3 Adaptive Control of Heat Loss

Mammals use a range of physiological and behavioural mechanisms to increase heat loss during exposure to heat, including increases in evaporative heat loss, adoption of specific behaviours and body postures, and changes in daily patterns of activity and social group dynamics. In extreme heat, mammals rely on the most powerful form of heat loss, evaporative water loss, via panting or sweating. While the evaporation of water from the respiratory tract or general skin surface can help to maintain core body temperature, it also creates osmotic strain, and as such the welfare implications of heat stress are context dependent. Hot and humid conditions are more stressful than hot and dry conditions, because evaporation requires a vapour pressure (humidity) gradient. High absolute humidity reduces the amount of heat that an animal can dissipate by evaporative water loss. To increase evaporative water loss, the animal exposed to heat stress needs to have access to drinking water to avoid dehydration.

In hot conditions, grazing animals adopt behaviours that promote passive heat loss by convection and radiation, preferring, for example, areas with high wind speed and shaded areas where they can avoid direct solar radiation. Cattle exposed to heat stress will prefer to stand instead of lying down, and sheep spread their hind legs thereby exposing the well-vascularised skin under the flanks and promoting convective heat loss (Campbell et al. 1969). During prolonged exposure to high temperatures, cattle, bison, goats, and sheep change their daily activity pattern, shifting grazing activity to the coolest hours of the day (evening) and even switching to nocturnal grazing (Vallentine 2000). In cattle, breed has a strong effect on the impact of hot conditions. *Bos primigenius indicus* cattle are well adapted to heat, and breeds of indicus cattle and those derived from crosses with European breeds (Brahman and Tuli for example) spend less time in the shade and more time grazing than European breeds such as Angus (Forbes et al. 1998).

Heat stress may have a greater impact on welfare than cold stress because the 'safety margin' between normal core temperature and lethal hyperthermia is smaller than that for lethal hypothermia. In addition to the impact on welfare, exposure to heat and cold stress causes a decrease in production, because thermoregulation, directly or indirectly, costs energy. For example, it has been estimated that thermal stress could account for an increase of about 40 % in the maintenance energy requirements of range beef cows (Ames 1985). While thermoregulatory costs are reflected in decreased productivity (Webster 1991), the maintenance requirements of ruminants increase linearly during cold stress but exponentially during heat stress (Ames and Ray 1983). In cattle in the Southern USA, fertility is reduced from around 50 % in winter to less than 15 % in the summer (Thatcher and Collier 1986). At the extremes of climatic conditions it is not just productivity that decreases, but the animals themselves can be at risk.

7.6 Challenge 4: Pressure from Environmental Fauna

In extensive systems, livestock share the environment with other animals that either compete for the same resources, prey on them, or parasitise them. In all cases, herbivores have adaptive responses, but these responses are not always optimal and can compromise both their welfare and productivity.

7.6.1 Competition for Resources

According to niche theory, all species differ to some extent in the resources they use (Prins and Fritz 2008). In mammalian herbivore assemblages, different species of herbivores can be classified into grazers, browsers, and mixed feeders because of differences in morphophysiological adaptations and 'feeding types' (Hofmann 1984, 1989). Therefore, cohabitation between two species with morphophysiological differences will not translate to an overlap among their diets. In contrast, if two or more herbivore species have similar morphophysiological adaptations, they will share food resources and, in periods of short supply, the performance of at least one of the species will decrease (Mishra et al. 2004). The intensity of resource competition is greater in areas of low productivity or during periods of low resource availability (e.g. in seasonal environments during the dry season). As an animal species gets outcompeted from preferred resources, it is likely that members will increase the consumption of less suitable forage (Gordon and Illius 1989), which in turn will negatively impact their nutrition and welfare. However, the presence of competitors can also have a positive effect on diet quality of livestock if the resources are abundant, a phenomena called facilitation. For example, the presence of wild ungulates depressed the food intake and performance of cattle during the dry season (competition), but their presence enhanced diet quality and performance of cattle during the wet season (facilitation; Odadi et al. 2011). In the Serengeti, buffalo and zebra feed on and trample taller and coarser grasses, clearing the way for smaller herbivores (e.g. gazelle) to feed on exposed plant parts of higher nutritional quality (Bell 1971). In extensive systems, it is possible that the feeding behaviours of one species improve the feeding efficiency of individuals of one or more coexisting species. Thus, some wild and domestic species may improve their welfare and nutrition through facilitative interactions (Prins and Fritz 2008; duToit 2011).

7.6.2 Cost of Predation

In addition to the obvious impacts of predators directly killing herbivores (i.e. lethal effects), predators have significant nonlethal impacts on their prey (Edwards 1983; Hernández and Laundré 2005). They may scare their prey, not just when they are about to attack (Brown et al. 1999), but they establish a 'landscape of fear' for herbivores with a topography determined by the level of perceived predation risk (Laundré et al. 2001). The response of herbivores to predator presence impacts on their feeding behaviour, nutritional status, and social structure, all potentially leading to decreased welfare. In the presence or perception of predators, herbivores sacrifice feeding effort and invest more time in vigilance and shift from riskier to safer feeding stations (Edwards 1983; Hernández and Laundré 2005). For example, in elk, the reintroduction of wolves into Yellowstone National Park has led to an increase in vigilance and a decrease in feeding rates (Laundré et al. 2001). The estimated 20 % decline in foraging effort by female elk compromised survival rates and led to a decrease in the birth mass of calves during the spring (Laundré et al. 2001).

Predator presence, or the perception of predator pressure, impacts on the quality of the forage consumed by herbivores. In the absence of predation, the prey selects the highest quality habitats, but in response to predators, the prey moves to poorer quality habitat, resulting in decreased diet quality (Edwards 1983). For instance, elk in Yellowstone National Park now use forest edge areas more than open meadows, although elk preferred open meadow areas before the release of wolves in the park (Hernández and Laundré 2005). Together the 'lost opportunities' to feed in profitable patches, which are presumably perceived as risky and the increase in time and effort invested in vigilance and apprehension, lead to an increase in the energy cost of predation by reducing nutrient intake and increasing energy expenditure. Even small changes in habitat may lead to large increases in the cost of predation (Brown and Kotler 2004). When the predation pressure increases so much that the animals are not able to meet their nutritional requirements, both productivity and welfare can be dramatically compromised. To assess and manage the impact of predation, in addition to accounting for the killing of animals, it is possible to measure the times at which herbivores quit eating a preferred forage, activity levels in time and space, and habitat distributions with and without perceived predation risk (Brown and Kotler 2004).

7.6.3 Parasitic Insects

In extensive systems, it is not possible to control for insect infestation, such as flies. The effect of insects can be direct, such as the Australian sheep blowfly (*Lucilia cuprina*) that is responsible for initiating most blowfly strikes, or indirect, such as flies causing continuous irritation that led to a reduction in grazing time and a decrease in nutrient intake (Lefcourt and Schmidtmann 1989). In bad seasons, sheep may lose a large amount of grazing time due to harassment by *Oestrus ovis* flies (Blood et al. 1983). Ungulates have adopted individual and group behaviours to reduce fly irritation. By lying down, animals reduce the exposure of body surfaces, decrease the production of some fly attractants (e.g. sweat and carbon dioxide), and dislodge fewer flies from foliage (Espmark and Langvatn 1979). When forage conditions are poor, animals need to increase their grazing time, walk more while grazing, and have difficulty to lie down and avoid fly irritation. Social grouping is also used as a means to reduce fly harassment. As groups become larger, each individual attracts fewer flies (e.g. Duncan and Vigne 1979). Social grouping creates a clear conflict with the increased dispersion of animals associated with poor forage conditions.

7.7 Knowledge Gaps

Within the Five Freedom framework, it is clear that a lack of nutrients and restriction in feed availability and quality, induced by either management decisions, pasture quality, environmental factors such as climate or interactions with other species, is a source of metabolic stress that compromises welfare. At the same time, the impact on welfare of unbalanced nutrition because of lack of diversity or the impact of PSC is unknown. It is also not clear whether incidental restriction and/or augmentation induce stress in livestock grazing on rangelands. Studies to answer this question will need to be able to assess the level of stress of large numbers of animals dispersed in large areas.

In this chapter, we have often said that livestock can be moved to an environment different from that in which they have evolved, thus creating a mismatch between the adaptive capacity and the environmental pressures. However, over the last 15 years numerous studies have shown that experience early in life can cause epigenetic changes that influence foraging behaviour, habitat selection, and animal health (Provenza 2008). For example, lambs exposed to a high-sodium-containing shrub during uterine life grow faster and handle a salt load better than lambs from mothers on pasture (Chadwick et al. 2009). Epigenetic effects suggest that future generations of livestock could be better adapted to the environment than their parents, and that experience has the potential to improve nutrition and welfare in the same habitat. To take full advantage of these rapid adaptive processes, we need to understand how important early life experiences are in the adaptation of an animal to low-quality diets and/or harsh environments. Should we change the environment in order to increase animal productivity and welfare, or shape an animal (i.e. through experiences in utero and early in life) to better fit its environment?

Livestock that graze in extensive systems are generalist herbivores, meaning that they evolved consuming diverse diets as opposed to monotonous pastures. Single foods generate orosensorial and postingestive signals that cause animals to satiate (Rolls 1986), and satiety may be aversive (Provenza 1996; Provenza and Villalba 2006). In addition, diverse diets increase the likelihood of ingesting beneficial chemicals that enhance the health and welfare of animals (Villalba et al. 2010a). However, the effects of exposure to low- vs. high-diversity diets on stress, health, and animal welfare are unknown.

The interactions between dispersion, increased grazing time, and the expression of other behaviours need to be explored to understand how grazing in extensive systems can decrease the richness and increase the metabolic cost of natural behaviours. For instance, courtship in free-ranging cattle involves a great deal of interaction between animals (Blockey 1976) that requires time and energy and, therefore, may increase stress and reduce production.

The impact of PSC on animal health, welfare, and productivity is receiving an increasing interest. However, only a few compounds have been studied and we do not know much about the optimal dosage, the efficiency of mixture, or even the amount that is consumed and how PSC are metabolised (Provenza and Villalba 2006). Research on the impact of detoxification pathways on diet selection and energetic costs conducted on possums (e.g. Marsh et al. 2006; Nersesian et al. 2011) and woodrats (e.g. Sorensen et al. 2005) is needed on ungulates grazing on rangelands. New studies should explore the effects of specific compounds, doses, and interactions, particularly in animals grazing in extensive systems where PSC are abundant and diverse. Then, we will be able to minimise the health risks and possibly improve the welfare and productivity of animals grazing in rangelands through better preparation and management of animals. To do so, we need to test and monitor novel plants and new plant varieties using bioassays and with animals under experimental conditions prior to them being introduced into grazing systems (Revell and Revell 2007). In addition to these direct effects of PSC on animal health, we need to quantify the metabolic cost associated with the neutralisation/detoxification of PSC by herbivores as well as to explore their ability to select diets that meet their nutritional requirements, while avoiding intoxication by PSC (Jensen et al. 2015).

While ambient conditions above and below the thermoneutral zone are described as heat and cold stress, the relationship between imposed thermal stress and animal welfare is more complex than simply assuming that thermal stress causes decreased welfare. The complexity of the adaptive response of herbivores to extreme temperature under extensive system conditions and the importance of breed on the long-term adaptation to climate change are poorly understood.

The long-term effects of a particular management regime need to be evaluated in order to better predict the nutrition and welfare of animals in the long run. For instance, supplementation programs at high stocking densities may be beneficial for animals in the short run. However, the negative long-term effects on rangelands due to overgrazing will certainly impact the nutrition and welfare of animals in the future.

7.8 Conclusions

Many of the challenges described in this chapter are rooted in the variability and unpredictability of the environment. Foods, habitats, and environmental conditions are not ‘provided’ by the manager, but they occur naturally. The challenge for managers is to provide the conditions and flexibility in their operations that allow animals to express their behaviour and cope with challenges in a way that production and welfare are maximised given the constraints imposed by the ever-changing environmental conditions.

The environmental challenges that animals experience in extensive conditions may represent a source of ‘positive stress’ if animals possess the experience and resources to effectively solve the problems with which they are presented (Meehan and Mench 2007). Thus, some of the challenges that herbivores experience in extensive conditions may become opportunities for managers to create innovative programs that provide animals the training and resources to rectify their states of unbalance, which will ultimately enrich the environment where animals live.

References

Adams DC (1987) Influence of winter weather on range livestock. In: Proceedings of the Grazing Livestock Nutrition Conference, University of Wyoming, Laramie, WY, pp 1037–1042

Adams DC, Nelsen TC, Reynolds WL, Knapp BW (1986) Winter grazing activity and forage intake of range cows in the northern great plains. J Anim Sci 62:1240–1246

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Akkari H, Ben Salem H, Gharbi M, Abidi S, Darghouth MA (2008) Feeding *Acacia cyanophylla* Lindl. foliage to Barbarine lambs with or without PEG: effect on the excretion of gastro-intestinal nematode eggs. Anim Feed Sci Technol 147:182–192

Allison CD (1985) Factors affecting forage intake by range by range ruminants: a review. J Range Manage 38:305–311

Ames DR (1980) Thermal environment affects production efficiency of livestock. Bioscience 30 (7):457–460

Ames DR (1985) Managing cows during winter. In: Proceedings of The Range Beef Cow Symposium IX, Chadron, NE, pp 11–16

Ames DR, Ray DE (1983) Environmental manipulation to improve animal productivity. J Anim Sci 57:209–220

Appleby MC (1996) Can we extrapolate from intensive to extensive conditions? Appl Anim Behav Sci 49:23–27

Arnold GW (1985a) Ingestive behaviour. In: Fraser AF (ed) Ethology of farm animals. Elsevier, Amsterdam, 500 pp

Arnold GW (1985b) Territoriality. In: Fraser AF (ed) Ethology of farm animals. Elsevier, Amsterdam, 500 pp

Arnold GW, Dudzinski ML (1978) Ethology of free ranging domestic animals. Elsevier, Amsterdam, 198 pp

Arnold GW, Maller RA (1977) Effects of nutritional experience in early and adult life on the performance and dietary habits of sheep. Appl Anim Ethol 3:5–26

Arriaga-Jordan CM, Holmes W (1986) The effect of concentrate supplementation on high-yielding dairy cows under two systems of grazing. J Agric Sci (Camb) 107:453–461

Aslani MR, Movassaghi AR, Mohri M, Abbasian A, Zarehpour M (2004) Clinical and pathological aspects of experimental oleander (*Nerium oleander*) toxicosis in sheep. Vet Res Commun 28:609–616

Athanasiadou S, Kyriazakis I, Jackson F, Coop RL (2001) Direct anthelmintic effects of condensed tannins towards different gastrointestinal species: in vitro and in vivo studies. Vet Parasitol 99:205–219

Bailey DW, Brown JR (2011) Rotational grazing systems and livestock grazing behavior in shrub-dominated semi-arid and arid rangelands. Rangel Ecol Manage 64:1–9

Bailey DW, Provenza FD (2008) Mechanisms determining large-herbivore distribution. In: Prins HHT, van Langevelde F (eds) Resource ecology: spatial and temporal dynamics of foraging. Springer, Dordrecht, pp 7–28

Bell RHV (1971) A grazing ecosystem in the Serengeti. Sci Am 225:86–93

Bernhoft A (2010) A brief review. In: Bernhoft A (ed) Bioactive compounds in plants—benefits and risks for man and animals. Nor Acad Sci Lett, Oslo, pp 11–17

Birrell HA (1991) The effect of stocking rate on the grazing behaviour of Corriedale sheep. Appl Anim Behav Sci 28:321–331

Blache D, Maloney SK, Revell D (2008) Use and limitations of alternative feed resources to sustain and improve reproductive performance in sheep and goats. Anim Feed Sci Technol 147:140–157

Blache D, Maloney SK, Terlouw EMC (2011) Physiology. In: Appleby MC, Hughes BO, Mench JA, Olsson A (eds) Animal welfare. CAB International, Wallingford, pp 155–182

Blackshaw JK, Blackshaw AW (1994) Heat stress in cattle and the effect of shade on production and behaviour: a review. Aust J Exp Agric 34:285–295

Blanc F, Theriez M (1998) Effects of stocking density on the behaviour and growth of farmed red deer hinds. Appl Anim Behav Sci 56:297–307

Blockey MA d B (1976) Sexual behaviour of bulls at pasture: a review. Theriogenology 6:387–392

Blood DC, Radostis OM, Henderson JA (1983) Veterinary medicine. Bailliere Tindall, Eastbourne

Bodas R, López S, Fernandez M, García-González R, Rodríguez AB, Wallace RJ, González JS (2008) In vitro screening of the potential of numerous plant species as antimethanogenic feed additives for ruminants. Anim Feed Sci Technol 145:245–258

Brody S (1945) Bioenergetics and growth. Reinhold, New York, NY, 786 pp

Broom DM (1986) Indicators of poor welfare. Br Vet J 142:524–526

Broom DM (1991) Animal welfare: concepts and measurement. J Anim Sci 69:4167–4175

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–2014

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399

Brunet S, Martinez-Ortiz de Montellano C, Torres-Acosta JFJ, Sandoval-Castro CA, Aguilar-Caballero AJ, Capetillo-Leal C, Hoste H (2008) Effect of the consumption of Lysiloma latisiliquum on the larval establishment of gastrointestinal nematodes in goats. Vet Parasitol 157:81–88

Burlison AJ, Hodgson J, Illius AW (1991) Sward canopy structure and the bite dimensions and bite weight of grazing sheep. Grass Forage Sci 46:29–38

Campbell JB, Stringham E, Gervais P (1969) Pasture activities of cattle and sheep. In: Campbell JB (ed) Experimental methods for evaluating herbage. Canada Department of Agriculture, Publication 1315

Campbell BM, Gordon IJ, Luckert MK, Petheram L, Vetter S (2006) In search of optimal stocking regimes in semi-arid grazing lands: one size does not fit all. Ecol Econ 60:75–85

Campling RC (1966) A preliminary study of the effect of pregnancy and of lactation on the voluntary intake of food by cows. Br J Nutr 20:25–39

Carulla JE, Kreuzer M, Machmuller A, Hess HD (2005) Supplementation of *Acacia mearnsii* tannins decrease methanogenesis and urinary nitrogen in forage-fed sheep. Aust J Agric Res 56:961–970

Catanese F, Obelar M, Villalba JJ, Distel RA (2013) The importance of diet choice on stress-related responses by lambs. Appl Anim Behav Sci 148:37–45

Chadwick MA, Vercoe PV, Williams IH, Revell DK (2009) Programming sheep production on saltbush: adaptations of offspring from ewes that consumed high amounts of salt during pregnancy and early lactation. Anim Prod Sci 49:311–317

Charcon E, Stobbs TH (1976) Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. Aust J Agric Res 27:709–727

Cowan MM (1999) Plant products as antimicrobial agents. Clin Microbiol Rev 12:564–582

Dawson TJ, Denny MJS, Russell EM, Ellis B (1975) Water usage and diet preferences of free ranging kangaroos, sheep and feral goats in the Australian arid zone during summer. J Zool 177:1–23

de Boever JL, Andries JI, de Brabander DL, Cottyn BG, Buysse FX (1990) Chewing activity of ruminants as a measure of physical structure. A review of factors affecting it. Anim Feed Sci Technol 27:281–291

De Villiers JF, Botha WA, Wandrag JJ (1994) The performance of lambs on kikuyu as influenced by stocking rate and grazing system. S Afr J Anim Sci 24:133–139

Deswysen AG (1986) Physiologie digestive comparee et valeur alimentaire des ensilages. Effect des acides acetique et lactique. In: Sanofi Animal Health (ed) L'ensilage: nouveaux aspects biologiques, Paris, 231 pp

Deswysen AG, Ellis WC, Pond KR (1987) Interrelationships among voluntary intake, eating and ruminating behaviour and ruminal motility of heifers fed corn silage. J Anim Sci 64:835–841

Dudzinski ML, Schuh HJ, Wilcox D, Gardiner G, Morrissey T (1978) Statistical and probabilistic estimations of forage conditions from grazing behaviour of Merino sheep in a semi-arid environment. Appl Anim Ethol 4:357–368

Dumont B, Garel JP, Ginane C, Decuq F, Farruggia A, Pradel P, Rigolot C, Petit M (2007) Effect of cattle grazing a species-rich mountain pasture under different stocking rates on the dynamics of diet selection and sward structure. Animal 1:1042–1052

Duncan IJH, Fraser D (1997) Understanding animal welfare. In: Appleby MC, Hughes BO (eds) Animal welfare. CAB International, Wallingford, pp 19–31

Duncan P, Vigne N (1979) The effect of group size in horses on the rate of attacks by blood-sucking flies. Anim Behav 27:623–625

Duncan AJ, Young SA (2002) Can goats learn about foods through conditioned food aversions and preferences when multiple food options are simultaneously available? J Anim Sci 80:2091–2098

Durmic Z, Blache D (2012) Bioactive plants and plant products: effects on animal function, health and welfare. Anim Feed Sci Technol 176:150–162

DuToit JT (2011) Coexisting with cattle. Science 333:1710–1711

Dziba LE, Hall JO, Provenza FD (2006) Feeding behavior of lambs in relation to kinetics of 1,8-cineole dosed intravenously or into the rumen. J Chem Ecol 32:391–408

Edwards PJ (1980) The use of stocking rate/animal performance models in research and extension. Proc Grassld Soc S Afr 15:73–77

Edwards J (1983) Diet shifts in moose due to predator avoidance. Oecologia 60:185–189

Egan AR (1980) Host animal-rumen relationships. Proc Nutr Soc 39:79–87

El Aich A, Rittenhouse LR (1988) Use of habitats by free-grazing sheep. Appl Anim Behav Sci 21:223–231

El Aich A, El Asraoui M, Rittenhouse LR (1991) Effect of trailing to water on temporal behaviour and ingestion of herded sheep in Morocco. Appl Anim Behav Sci 31:251–257

Espmark Y, Langvatn R (1979) Lying down as a means of reducing fly harassment in red deer (*Cervus elaphus*). Behav Ecol Sociobiol 5:51–54

Estell RE (2010) Coping with shrub secondary metabolites by ruminants. Small Rumin Res 94:1–9

FAO (2009) The state of food and agriculture 2009. Livestock in the balance. FAO, Rome

Farm Animal Welfare Council (1993) Second report on priorities for research and development in farm animal welfare. MAFF, Tolworth

Ferme D, Banjac M, Calsamiglia S, Busquet M, Kamel C, Avgustin G (2004) The effects of plant extracts on microbial community structure in a rumen-simulating continuous-culture system as revealed by molecular profiling. Folia Microbiol (Praha) 49:151–155

Flores ER, Provenza FD, Balph DF (1989a) Role of experience in the development of foraging skills of lambs browsing the shrub servicerry. Appl Anim Behav Sci 23:271–278

Flores ER, Provenza FD, Balph DF (1989b) Relationship between plant maturity and foraging experience of lambs grazing hycrest crested wheatgrass. Appl Anim Behav Sci 23:279–284

Flores ER, Provenza FD, Balph DF (1989c) The effect of experience on the foraging skills of lambs: importance of plant form. Appl Anim Behav Sci 23:285–291

Foley WJ, McLean S, Cork SJ (1995) Consequences of biotransformation of plant secondary metabolites on acid-base metabolism in mammals—a final common pathway? J Chem Ecol 21:721–743

Foley WJ, Iason GR, McArthur C (1999) Role of plant secondary metabolites in the nutritional ecology of mammalian herbivores-how far have we come in 25 years? In: Jung HJG, Fahey GC Jr (eds) Nutritional ecology of herbivores, 5th International Symposium on the Nutrition of Herbivores. American Society of Animal Science, Savoy, IL, pp 130–209

Forbes JM (2007) A personal view of how ruminant animals control their intake and choice of food: minimal total discomfort. Nutr Res Rev 20:132–146

Forbes TD, Rouquette FM, Holloway JW (1998) Comparisons among Tuli-, Brahman-, and Angus-sired heifers: intake, digesta kinetics, and grazing behavior. J Anim Sci 76:220–227

Fowler DG (1984) Reproductive behaviour of rams. In: Lindsay DR, Pearce DT (eds) Reproduction in sheep. Cambridge University Press, Cambridge, pp 39–46, 414 pp

Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. Am Nat 108:269–286

Freeland WJ, Calcott PH, Anderson LR (1985) Tannins and saponin: interaction in herbivore diets. Biochem Syst Ecol 13:189–193

Fretwell SD, Lucas HL Jr (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor 19:16–36

Gaughan JB, Mader TL, Holt SM, Sullivan ML, Hahn GL (2009) Assessing the heat tolerance of beef cattle genotypes. Int J Biometeorol 54(6):617–627

Gill J, Campling RC, Westgarth DR (1966) A study of chewing during eating in the cow. Br J Nutr 20:13–23

Gonyou HW (1986) Assessment of comfort and well-being in farm animals. J Anim Sci 62:1769–1775

Gordon IJ, Illius AW (1989) Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383–389

Gradé JT, Tabuti JRS, Van Damme P (2009) Four footed pharmacists: indications of self-medicating livestock in Karamoja, Uganda. Econ Bot 63:29–42

Greathead H (2003) Plants and plant extracts for improving animal productivity. Proc Nutr Soc 62:279–290

Gregorini P, Villalba JJ, Provenza FD, Beukes PC, Forbes JM (2015) Modelling preference and diet selection patterns by grazing ruminants: a development in a mechanistic model of a grazing dairy cow, MINDY. Anim Prod Sci 55:360–375

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester, 456 pp

Grissom G, Steffens T (2013) Adaptive grazing management at Rancho Largo Cattle Company. Rangelands 35:35–44

Grummer RR, Jacob AL, Woodford JA (1987) Factors associated with variation in milk fat depression resulting from high grain diets fed to dairy cows. J Dairy Sci 70:613–619

Hahn G (1999) Dynamic responses of cattle to thermal heat loads. J Anim Sci 77(Suppl 2):10–20

Hall SJG, Moore GF (1986) Feral cattle of Swona, Orkney Islands. Mammal Rev 16:9–96

Hansen PJ (2004) Physiological and cellular adaptations of zebu cattle to thermal stress. Anim Reprod Sci 82:349–360

Hart KJ, Yanez-Ruiz DR, Duval SM, McEwan NR (2007) Plant extracts to manipulate rumen fermentation. Anim Feed Sci Technol 147:8–35

Hernández L, Laundré JW (2005) Foraging in the ‘landscape of fear’ and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. Wildl Biol 11:215–220

Hernández-Villegas MM, Borges-Argáez R, Rodriguez-Vivas RI, Torres-Acosta JFJ, Méndez-Gonzalez M, Cáceres-Farfan M (2011) Ovicidal and larvicidal activity of the crude extracts from *Phytolacca icosandra* against *Haemonchus contortus*. Vet Parasitol 179:100–106

Hodgson J (1990) Grazing management: science into practice. Longman, Essex, 203 pp

Hodgson J, Illius AW (1996) The ecology and management of grazing systems. CAB International, Oxford, 466 pp

Hofmann RR (1984) Comparative anatomical studies imply adaptive variations of ruminant digestive physiology. Can J Anim Sci 64(Suppl):203–205

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants. A comparative view of their digestive system. Oecologia 78:443–457

Holmes W (1989) The utilization of pasture. In: Jarrige R (ed) Ruminant nutrition: recommended allowances and feed tables. INRA, Paris, 389 pp

Hooper AP, Welch JG (1983) Chewing efficiency and body size of kid goats. J Dairy Sci 66:2551–2556

Hoskin SO, Barry TN, Wilson PR, Charleston WAG, Hodgson J (1999) Effects of reducing anthelmintic input upon growth and faecal egg and larval counts in young farmed deer grazing chicory (*Cichorium intybus*) and perennial ryegrass (*Lolium perenne)*/white clover (*Trifolium repens)* pasture. J Agric Sci (Camb) 132:335–345

Houpt KA (1991) Domestic animal behavior for veterinarians and animal scientists, 2nd edn. Iowa State University Press, Ames, IA, 416 pp

Houpt KA, Zahorik DM, Swartzman-Andert JA (1990) Taste aversion learning in horses. J Anim Sci 68:2340–2344

Hunter RF, Milner C (1963) The behaviour of individual, related and groups of South Country Cheviot hill sheep. Anim Behav 11:507–513

Hutton PG, Durmic Z, Vercoe PE (2010) Investigating Eremophila glabra as a bioactive agent for preventing lactic acidosis in sheep. Anim Prod Sci 50:449–453

Illius AW, Jessop NS (1995) Modeling metabolic costs of allelochemical ingestion by foraging herbivores. J Chem Ecol 21:693–719

Ingebrigtsen K (2010) Main plant poisonings in livestock in the Nordic countries. In: Bernhoft A (ed) Bioactive compounds in plants—benefits and risks for man and animals. Norwegian Academy of Science and Letters, Oslo, pp 30–43

Iups Thermal Commission (2001) Glossary of terms for thermal physiology: third edition. Jpn J Physiol 51:245–280

Jackson F, Miller J (2006) Alternative approaches to control—Quo vadit? Vet Parasitol 139:371–384

Jensen LM, Wallis IR, Foley WJ (2015) The relative concentrations of nutrients and toxins dictate feeding by a vertebrate browser, the greater glider *Petauroides volans*. PLoS One 10:e0121584

Jessen C (2001) Temperature regulation in humans and other mammals. Springer, Berlin, 193 pp

Juhnke J, Miller J, Hall JO, Provenza FD, Villalba JJ (2012) Preference for condensed tannins by sheep in response to challenge infection with Haemonchus contortus. Vet Parasitol 188:104–114

Kayser O, Kiderlen AF, Croft SL (2003) Natural products as antiparasitic drugs. Parasitol Res 90: S55–S62

Key C, MacIver RM (1980) The effects of maternal influences on sheep: breed differences in grazing, resting and courtship behavior. Appl Anim Ethol 6:33–48

Kilgour R, Pearson AJ, de Langen H (1975) Sheep dispersal patterns on hill country: techniques for study and analysis. Proc N Z Soc Anim Prod 35:191–197

Kumar D, Kumar A, Prakash O (2012) Potential antifertility agents from plants: a comprehensive review. J Ethnopharmacol 140:1–32

Kyriazakis I, Oldham JD (1993) Diet selection in sheep: the ability of growing lambs to select a diet that meets their crude protein (nitrogen × 6.25) requirements. Br J Nutr 69:617–629

Kyriazakis I, Savory CJ (1997) Hunger and thirst. In: Appleby MC, Hughes BO (eds) Animal welfare. CAB International, Wallingford, pp 49–62

Landau S, Azaizeh H, Muklada H, Glasser T, Ungar ED, Baram H, Abbas N, Markovics A (2010) Anthelmintic activity of Pistacia lentiscus foliage in two Middle Eastern breeds of goats differing in their propensity to consume tannin-rich browse. Vet Parasitol 173:280–286

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Can J Zool 79:1401–1409

Lawrence AB, Wood-Gush DGM (1987) Social behaviour of hill sheep; more to it than meets the eye. Appl Anim Behav Sci 17:382

Lawrence AB, Wood-Gush DGM (1988) Influence of social behaviour on utilization of supplemental feedblocks by Scottish hill sheep. Anim Prod 46:203–212

Lefcourt AM, Schmidtmann ET (1989) Body temperature of dry cows on pasture: environmental and behavioural effects. J Dairy Sci 72:3040–3049

Lobley GE, Milano GD (1997) Regulation of hepatic nitrogen metabolism in ruminants. Proc Nutr Soc 57:547–563

Lu CD, Jorgensen NA (1987) Alfalfa saponins affect site and extent of nutrient digestion in ruminants. J Nutr 117:919–927

Lu CD (1988) Grazing behaviour and diet selection of goats. Small Rumin Res 1:205–216

Lynch JJ (1974) Merino sheep: some factors affecting their distribution in very large paddocks. In: Geist V, Walther F (eds) The behaviour of ungulates and its relation to management, New series. No. 24. IUCN, Morges, pp 679–707

Lynch JJ, Mottershead BE, Alexander G (1980) Sheltering behaviour and lamb mortality amongst shorn Merino ewes lambing in paddocks with a restricted area of shelter or no shelter. Appl Anim Ethol 6:163–174

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Mahgoub O, Kadim IT, Tageldin MH, Al-Marzooqi WS, Khalaf SQ, Ambu Ali A (2008) Clinical profile of sheep fed non-conventional feeds containing phenols and condensed tannins. Small Rumin Res 78:115–122

Manteca X, Villalba JJ, Atwood SB, Dziba L, Provenza FD (2008) Is dietary choice important to animal welfare? J Vet Behav 3:229–239

Marai IFM, El-Darawany AA, Fadiel A, Abdel-Hafez MAM (2007) Physiological traits as affected by heat stress in sheep—a review. Small Rumin Res 71:1–12

Marsh KJ, Wallis IR, McLean S, Sorensen JS, Foley WJ (2006) Conflicting demands on detoxification pathways influence how common brushtail possums choose their diets. Ecology 87:2103–2112

Martínez-Ortiz-de-Montellano C, Vargas-Magaña JJ, Canul-Ku HL, Miranda-Soberanis R, Capetillo-Leal C, Sandoval-Castro CA, Hoste H, Torres-Acosta JFJ (2010) Effect of a tropical tannin-rich plant *Lysiloma latisiliquum* on adult populations of *Haemonchus contortus* in sheep. Vet Parasitol 172:283–290

Mazid M, Khan TA, Mohamad F (2011) Role of secondary metabolites in defence mechanism in plants. Biol Med 3:232–249

McAllister RRJ (2012) Livestock mobility in arid and semiarid Australia: escaping variability in space. Rangel J 34:139–147

McGaw LJ, Eloff JN (2008) Ethnoveterinary use of southern African plants and scientific evaluation of their medicinal properties. J Ethnopharmacol 119:559–574

McGlone JJ (2001) Farm animal welfare in the context of other society issues: toward sustainable systems. Livest Prod Sci 72:75–81

Meehan CL, Mench JA (2007) The challenge of challenge: can problem solving opportunities enhance animal welfare? Appl Anim Behav Sci 102:246–261

Min BR, Hart SP (2003) Tannins for suppression of internal parasites. J Anim Sci 81:E102–E109

Min BR, Pomroy WE, Hart SP, Sahlu T (2004) The effect of short-term consumption of a forage containing condensed tannins on gastro-intestinal nematode parasite infections in grazing wether goats. Small Rumin Res 51:279–283

Mishra C, vanWieren SE, Ketner P, Heitkonig MA, Prins HHT (2004) Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. J Appl Ecol 41:344–354

Nagy JG, Tengerdy RP (1968) Antibacterial action of essential oils of Artemisia as an ecological factor. II. Antibacterial action of the volatile oils of Artemisia tridentata (big sagebrush) on bacteria from the rumen of mule deer. Appl Microbiol 16:441–444

Nersesian CL, Banks PB, McArthur C (2011) Titrating the cost of plant toxins against predators: determining the tipping point for foraging herbivores. J Anim Ecol 80:753–760

Nicolson L (1984) Boran livestock in heavy drinking bouts. ILCA Newsletter (International Livestock Centre for Africa) 3:1–4. Addis Abeba, Ethiopia

Niezen JH, Robertson HA, Waghorn GC, Charleston WAG (1998) Production, faecal egg counts and worm burdens of ewe lambs which grazed six contrasting forages. Vet Parasitol 80:15–27

Niezen JH, Charleston WA, Robertson HA, Shelton D, Waghorn GC, Green R (2002) The effect of feeding sulla (Hedysarum coronarium) or lucerne (Medicago sativa) on lamb parasite burdens and development of immunity to gastrointestinal nematodes. Vet Parasitol 105:229–245

NRC (1981) Nutrient requirements of goats: angora, dairy and meat goats in temperate and tropical countries. National Academy Press, Washington, DC

O'Connor TG (1995) Transformation of a savanna grassland by drought and grazing. Afr J Range Forage Sci 12:53–60

Odadi WO, Karachi MK, Abdulrazak SA, Young TP (2011) African wild ungulates compete with or facilitate cattle depending on season. Science 333:1753–1755

Oh HK, Sakai T, Jones MB, Longhurst WM (1967) The effect of various essential oils isolated from Douglas-fir needles upon sheep and deer rumen microbial activity. Appl Microbiol 15:777–784

Oh HK, Jones MB, Longhurst WM (1968) Comparison of rumen microbial inhibition resulting from various essential oils isolated from relatively unpalatable plant species. Appl Microbiol 16:39–44

Osoro K, Mateos-Sanz A, Frutos P, Garcia U, Ortega-Mora LM, Ferreira LMM, Celaya R, Ferre I (2007) Anthelmintic and nutritional effects of heather supplementation on Cashmere goats grazing perennial ryegrass-white clover pastures. J Anim Sci 85:861–870

Osuji PO (1974) The physiology of eating and the expenditure of the ruminant at pasture. J Range Manage 27:437–447

Owen-Smith N, Novellie P (1982) What should a clever ungulate eat? Am Nat 119:151–178

Paolini V, Dorchies P, Hoste H (2003) Effects of sainfoin hay on gastrointestinal nematode infections in goats. Vet Rec 152:600–601

Patel DK, Kumar R, Prasad SK, Hemalatha S (2011) Pharmacologically screened aphrodisiac plant-A review of current scientific literature. Asian Pac J Trop Biomed 1:S131–S138

Patra AK, Saxena J (2009) Dietary phytochemicals as rumen modifiers: a review of the effects on microbial populations. Anton Leeuw 96:363–375

Pfister JA, Provenza FD, Manners GD, Gardner DR, Ralphs MH (1997) Tall larkspur ingestion: can cattle regulate intake below toxic levels? J Chem Ecol 23:759–777

Pfister JA, Provenza FD, Panter KE, Stegelmeier BL, Launchbaugh KL (2002) Risk management to reduce livestock losses from toxic plants. J Range Manage 55:291–300

Pfister JA, Gardner DR, Cheney CC, Panter KE, Hall JO (2010) The capability of several toxic plants to condition taste aversions in sheep. Small Rumin Res 90:114–119

Prins HH, Fritz H (2008) Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. In: Gordon IJ, Prins HH (eds) The ecology of browsing and grazing. Springer, Berlin, pp 179–200

Provenza FD (1996) Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. J Anim Sci 74:2010–2020

Provenza FD (2008) What does it mean to be locally adapted and who cares anyway? J Anim Sci 86:E271–E284

Provenza FD, Villalba JJ (2006) Foraging in domestic vertebrates: linking the internal and external milieu. In: Bels VL (ed) Feeding in domestic vertebrates: from structure to function. CABI, Oxfordshire, pp 210–240

Provenza FD, Villalba JJ (2010) The role of natural plant products in modulating the immune system: an adaptable approach for combating disease in grazing animals. Small Rumin Res 89:131–139

Provenza FD, Burritt EA, Clausen TP, Bryant JP, Reichardt PB, Distel RA (1990) Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. Am Nat 136:810–828

Raubenheimer D (1992) Tannic acid, protein, and digestible carbohydrate dietary imbalance and nutritional compensation in locusts. Ecology 73:1012–1027

Revell CK, Revell DK (2007) Meeting 'duty of care' obligations when developing new pasture species. Field Crop Res 104:95–102

Robertshaw D (2004) Temperature regulation and the thermal environment. In: Reece W (ed) Dukes' physiology of domestic animals. Cornell University Press, Ithaca

Rogosic J, Estell RE, Skobic D, Martinovic A, Maric S (2006) Role of species diversity and secondary compound complementarity on diet selection of Mediterranean shrubs by goats. J Chem Ecol 32:1279–1287

Rolls BJ (1986) Sensory-specific satiety. Nutr Rev 44:93–101

Rutter SM (2010) Review: grazing preferences of sheep and cattle: implications for production, the environment and animal welfare. Can J Anim Sci 90:285–293

Sardon D, de la Fuente I, Calonge E, Perez-Alenza MD, Castano M, Dunner S, Pena L (2005) H-ras immunohistochemical expression and molecular analysis of urinary bladder lesions in grazing adult cattle exposed to bracken fern. J Comp Pathol 132:195–201

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. Bioscience 37:789–799

Shaik SA, Terrill TH, Miller JE, Kouakou B, Kannan G, Kaplan RM, Burke JM, Mosjidis JA (2006) Sericea lespedeza hay as a natural deworming agent against gastrointestinal nematode infection in goats. Vet Parasitol 139:150–157

Sivakumaran S, Molan AL, Meagher LP, Kolb B, Foo LY, Lane GA, Attwood GA, Fraser K, Tavendale M (2004) Variation in antimicrobial action of proanthocyanidins from Dorycnium rectum against rumen bacteria. Phytochemistry 65:2485–2497

Sorensen JS, McLister JD, Dearing MD (2005) Novel plant secondary metabolites impact dietary specialists more than generalists (*Neotoma* spp.). Ecology 86:140–154

Squires V (1981) Livestock management in the arid zone. Inkata Press, Melbourne

Squires VR, Wilson AD (1971) Distance between food and water supply and its effects on drinking frequency, and food and water intake of Merino and Border Leicester sheep. Aust J Agric Res 22:283–290

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ, 262 pp

Stienezen GC, Waghorn GC, Douglas GB (1996) Digestibility and effects of condensed tannins on digestion of sulla (*Hedysarum coronarium*) when fed to sheep. N Z J Agric Res 39:215–221

Svendsen M, Ellingsen I, Tonstad S (2010) Compounds that may be responsible for reduced risk for cardiovascular diseases related to consumption of vegetables, fruit and berries. In: Bernhoft A (ed) Bioactive compounds in plants—benefits and risks for man and animals. Norwegian Academy of Science and Letters, Oslo, pp 71–77

Thatcher WW, Collier RJ (1986) Effects of climate on bovine reproduction. In: Morrow DA (ed) Current therapy in theriogenology, 2nd edn. W.B. Saunders, Philadelphia, PA, pp 301–309

Thomas DW, Samson C, Bergeron J (1988) Metabolic costs associated with the ingestion of plant phenolics by Microtus pennsylvanicus. J Mammal 69:512–515

Turner SP, Dwyer CM (2007) Welfare assessment in extensive animal production systems: challenges and opportunities. Anim Welf 16:189–192

Utsumi SA, Cibils AF, Estell RE, Soto-Navarro SA, Van Leeuwen D (2009) Seasonal changes in one seed juniper intake by sheep and goats in relation to protein and plant secondary metabolites. Small Rumin Res 81:152–162

Vallentine JF (2000) Grazing management, 2nd edn. Academic, San Diego, CA, 533 pp

Van Soest PJ, Mertens DR, Deinum B (1978) Preharvest factors influencing quality of conserved forage. J Anim Sci 47:712–720

Vercoe PE, Durmic Z, Revell DK (2009) Rumen microbial ecology: helping to change landscapes. Options Méditérr 85:225–236

Viegi L, Pieroni A, Guarrera PM, Vangelisti R (2003) A review of plants used in folk veterinary medicine in Italy as basis for a databank. J Ethnopharmacol 89:221–244

Villalba JJ, Provenza FD (1996) Preference for flavored wheat straw by lambs conditioned with intraruminal administrations of sodium propionate. J Anim Sci 74:2362–2368

Villalba JJ, Provenza FD (1997a) Preference for wheat straw by lambs conditioned with intraruminal infusions of starch. Br J Nutr 77:287–297

Villalba JJ, Provenza FD (1997b) Preference for flavored foods by lambs conditioned with intraruminal administrations of nitrogen. Br J Nutr 78:545–561

Villalba JJ, Provenza FD (1997c) Preference for flavored wheat straw by lambs conditioned with intraruminal infusions of acetate and propionate. J Anim Sci 75:2905–2914

Villalba JJ, Provenza FD, Hall JO, Peterson C (2006) Phosphorus appetite in sheep: dissociating taste from postingestive effects. J Anim Sci 84:2213–2223

Villalba JJ, Provenza FD, Hall JO (2008) Learned appetites for calcium, phosphorus and sodium in sheep. J Anim Sci 86:738–747

Villalba JJ, Provenza FD, Manteca X (2010a) Links between ruminants' food preference and their welfare. Animal 4:1240–1247

Villalba JJ, Provenza FD, Hall JO, Lisonbee LD (2010b) Selection of tannins by sheep in response to gastrointestinal nematode infection. J Anim Sci 88:2189–2198

Villalba JJ, Catanese F, Provenza FD, Distel RA (2011) Relationships between early experience to dietary diversity, acceptance of novel flavors, and open field behavior in sheep. Physiol Behav 105:181–187

Waghorn GC (2008) Beneficial and detrimental effects of dietary condensed tannins for sustainable sheep and goat production—progress and challenges. Anim Feed Sci Technol 147:116–139

Walker JW (1995) Viewpoint: grazing management and research now and in the next millennium. J Range Manage 48:350–357

Waller PJ (2006) Sustainable nematode parasite control strategies for ruminant livestock by grazing management and biological control. Anim Feed Sci Technol 126:277–289

Wallis de Vries MF, Schippers P (1994) Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. Oecologia 100:107–117

Wang CJ, Wang SP, Zhou H (2009) Influences of flavomycin, ropadiar, and saponin on nutrient digestibility, rumen fermentation, and methane emission from sheep. Anim Feed Sci Technol 148:157–166

Webster A (1991) Metabolic responses of farm animals to high temperature. In: Ronchi B, Nardone A, Boyazoglu J (eds) Animal husbandry in warm climates. Pudoc Wageningen, Viterbo, pp 15–22

Welch JG, Smith AM (1970) Forage quality and rumination time in cattle. J Dairy Sci 53:797–800

Williamson G, Payne WJA (1978) An introduction to animal husbandry in the tropics, 3rd edn. Longman, Essex, 881 pp

Wilson BJ, Garst JE, Linnabary RD, Channell RB (1977) Perilla ketone: a potent lung toxin from the mint plant, *Perilla frutescens* Britton. Science 197:573–574

Zimmerman EA (1980) Desert ranching in central Nevada. Rangelands 2:184–186