

## Chapter 2

# Factors Influencing Livestock Productivity

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**Abstract** Numerous factors affect livestock production and productivity. In this chapter we will address those that are of paramount importance: climate, nutrition, and health aspects. In initial section we will review the effects of climate on livestock productivity and provide examples of livestock adaptation to climate constraints such as the *Bos indicus* cattle breeds adapted to hot weather and the fat tailed sheep, particularly adapted to arid conditions. In subsequent sections we address the influence of diseases and parasitism on livestock production and provide specific case studies on how diseases and parasites conditions affect livestock productivity and how domestic animals have adapted in order to cope with them. Finally, we describe two major nutrition-related factors affecting livestock productivity: seasonal weight loss and the browsing vs. grazing abilities in ruminants at the level of the oral cavity. In all section, case studies are provided as examples of specific adaptations to these problems.

**Keywords** Livestock productivity • Climate • Health • Nutrition

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## 2.1 Introduction

Livestock systems occupy about 30% of the planet's ice-free terrestrial surface area and this sector is increasingly organized in long market chains employing approximately 1.3 billion people globally and directly supporting the livelihoods of 600 million smallholding farmers in the developing countries (Thornton 2010). Livestock production is therefore a key component of world agriculture. In fact, throughout the world, human populations largely depend on domestic animals for a multitude of purposes, essentially the production of meat, fat, milk, and other dairy products, eggs and fibers like wool or cashmere as well as other purposes such as transport, draft, and provision of fertilizers, especially in developing countries. Additionally, in some parts of the world West Africa, for example, farm animals particularly cattle are symbolic of an individual's wealth and status. Herders in Scandinavian Lapland largely depend on reindeer (*Rangifer tarandus*), (Ulvevadet and Hausner 2011) as the major source of protein, the Pacific Islanders largely depend on pig as the only source of meat while Andean cultures of South America depends on the Llama (*Lama glama*) for transport, milk, meat, and hides production (Markemann and Valle Zárate 2010). Although less conspicuous, the situation is analogous to the developed countries like Australia where merino sheep wool production is very advanced or United States and Canada with sophisticated cattle ranching, meat, and dairy production. Brazil and Argentina are examples of emerging countries with advanced meat and dairy production industry.

In such a context, livestock productivity is therefore of utmost importance as breeder's income, livelihoods, and ultimately the survival of entire populations and cultures relying on animal production. Numerous factors affect livestock productivity which is the main focus area of this book and also of the present chapter. Most of them will be dealt separately throughout this book. In the present chapter we will give a brief introduction to those factors that have the most significant and frequently limiting effects: Climate, Diseases and Parasites, and Nutrition.

The latter will be divided into two sections, the first deals with the effect of seasonal weight loss (SWL), the major drawbacks to animal production in tropical and Mediterranean climates, and the second details on adaptation of ruminants to different diets and particularly the difference between browsers and grazers in the adaptations to poor quality diets. In all sections examples are provided on how such factors impact livestock productivity. Furthermore, case studies depicting specific adaptation levels of farm animals to stress and other environmental factors are also provided.

## **2.2 Climate Influence on Livestock Productivity**

Of all the factors influencing livestock production, climate, and location are undoubtedly the most significant. In fact, climatology characteristics such as ambient temperature and rainfall patterns have great influence on pasture and food resources availability cycle throughout the year, and types of disease and parasite outbreaks among animal populations.

In the literature, there are numerous climate classifications types. The most widely used is the Köppen classification that roughly divides world climates under the following categories: Tropical (Group A), Dry (Group B), Temperate (Group C), Continental (Group D), Polar (Group E), and Alpine (Group H). Generally speaking, it is assumed that animal production is a vital economic activity in all categories with the exception of polar climates. These climate types pose important constraints to animal production, for example, uneven distribution of rainfall during rainy and dry (tropical), prolonged dry periods of several years (Dry), long and extremely cold winters (Temperate), long hot summers (Continental), or winters with a significant amount of snowfall (Alpine). Domestic animals that have been selected in such climate conditions have developed strategies in order to cope with factors associated with climate variability either by maintaining body temperature (homeostasis) under high or low environmental temperatures through a broad range of physiological responses; or by adapting to seasonal nutrition scarcity, in particular SWL through physiological and behavioral adaptations or by possessing the ability to tolerate endemic diseases and parasites that severely limit animal performance.

Tropical climate (Group A) is usually divided into 3 subgroups (Tropical rainforest, Monsoon and Tropical wet and dry, or Savannah). All three are characterized by dry and rainy seasons with different durations according to the geographical location, among other factors. In general, the rainy season is characterized by high ambient temperatures and humidity. To cope with such conditions, farm animals have developed several physiological strategies such as higher surface of skin area, localized fat depots, or behavioral strategies like late afternoon grazing and the search for shade. In cattle, such combination of strategies is extraordinarily evident and is therefore an interesting case study.

**Fig. 2.1** A *B. indicus* (zebu) bull indigenous to India. Contrary to European cattle (*B. taurus*), zebu cattle are particularly adapted to hot environments. Such trait is mainly achieved through a number of physiological adaptations such as the characteristic hump and presence of appendages, localized fat deposition, and a light coat color



Domestic cattle comprise two species, the European cattle (*Bos taurus*) and the Zebu or Indian cattle (*Bos indicus*), presented in Fig. 2.1. *B. taurus* was bred from the auroch, a wild bovid species existing in Eurasia until the nineteenth century and presently spread globally due to human settlements. On the contrary, *B. indicus* evolved in the Indian subcontinent but later spread to Africa, and to the Americas, the Pacific Islands and Australia around 300 years ago. It is generally accepted that both species share a common ancestor that at some point around 100,000 years ago diverged (Hansen 2004). Both species are however very similar, produce fertile hybrids and in fact numerous composite breeds of the two species exist. *B. indicus* cattle are particularly adapted to tropical environments, particularly to hot environments. Several studies on the comparison of zebu breeds and *B. taurus* breeds when subjected to high ambient temperatures are available in the literature (Barros et al. 2006; Collier et al. 2006, 2008), particularly originating from the United States, Brazil, and Australia, either under field conditions or more frequently in controlled environmental chambers (Barros et al. 2006) or gene expression studies (Collier et al. 2006, 2008). Additionally, zebu adaptation to heat stress has been thoroughly reviewed by Hansen (2004). To avoid increase in body temperature and maximize heat loss when animals are subjected to high ambient temperatures, the amount of heat produced by the body must equal to the amount dissipated to the surrounding environment. *B. indicus* rely on a combination of six strategies in order to accomplish this objective: (1) increasing surface area per unit of body weight; (2) increasing temperature gradient between animal and air; (3) increasing conduction of heat from the body core to the skin; (4) decreasing solar radiation reflection; (5) increasing metabolic rate and feed intake, and (6) adjusting cellular mechanisms.

Such a combination of strategies is achieved by a number of physiological abilities, as reviewed by Hansen (2004) and Berman (2011). Metabolic rate may be defined as the amount of energy produced by unit of surface area. *B. taurus* tend to have higher metabolic rates than *B. indicus*, as the latter are lighter, have proportionally smaller internal organs and tend to have larger body surface area. Zebu cattle also have a greater ability to produce sweat. In particular, in comparison to

*B. taurus* breeds, Zebu cattle have a higher density of larger and more superficially located sweat glands. Increases in sweat production allows zebu to dissipate more heat through sweating than *B. taurus*. A second adaptation lays in a higher resistance to outer influx of heat flow from the environment. This is achieved chiefly through the coat cover of *B. indicus* tending to be lighter in color, sleeker, and shinier in contrast to the darker, denser, and typically woolly coating of European cattle. Skin appendages are also an important and recognizable feature of *B. indicus* cattle. The main function of appendages is to increase the surface area of the skin therefore specifically contributing to the already mentioned lowering of the metabolic rate and the increase in the presence of sweat glands, hence reducing the amount of heat produced by the body and increasing heat dissipation. A very visible characteristic of all Zebu breeds is the cervo-thoracic hump. In *B. indicus*, hump fat allows decreased body fat deposition throughout the body, resulting in increased heat dissipation. Additionally, the hump is an additional appendage that contributes to the increase of body surface area. Zebu cattle reputedly utilize a series of mechanisms at the cellular and molecular level resulting in a greater adaptation to high environmental temperatures. Such mechanisms are poorly defined at present, however phenomena such as higher lymphocyte in vitro of Zebu cattle when exposed to higher ambient temperatures in comparison to European cattle. *B. indicus* are undoubtedly an interesting case study regarding adaptation to high ambient temperatures that make them the cattle type of choice for most of the extensive production systems in the tropics and subtropics. They are known for having higher tolerance to tick infestations and tick-borne diseases and also have greater capacity to digest fodders with high dietary fiber content when compared to *B. taurus*. Nevertheless, zebus are also regarded by breeders as animals with poorer productive performance with lower meat tenderness that significantly affects access to several export markets. Milk production is also considered to be poor with a persistent lactation. Finally, short estrus and long pre-pubertal periods and a characteristic difficult temperament rendering difficult herd management. Nevertheless, it is generally accepted that the ability to withstand and produce under hot temperatures clearly surpasses the above-mentioned inconveniences.

Group B (Dry climates) include deserts and steppe-like climates, encompassing large areas of all continents. Large areas in Africa, the Middle East and Central Asia have this type of climate which is characterized by rain seasonality and the existence of periods of prolonged droughts. In these vast areas, sheep production relies heavily on indigenous breeds with distinct anatomy namely fat tail and fat rump (see Fig. 2.2). These breeds are the main ovine genetic resource in the Middle East, North Africa, Iran, Pakistan, Central Asian Republics, China, Mongolia, East and Southern Africa and have important populations in agricultural export countries like Brazil and Australia (Almeida 2011a). With regards to international diffusion, only two fat tailed breeds may be classified as international: the Awassi breed originating from several Middle Eastern countries that was improved in Israel and dissipated to the rest of the world as a selected dairy breed (Gootwine 2011). The Karakul (*Astrakhan*) breed from the former Soviet

**Fig. 2.2** Fat tailed Damara sheep. This group of breeds is particularly adapted to extensive production systems in semi-arid environments

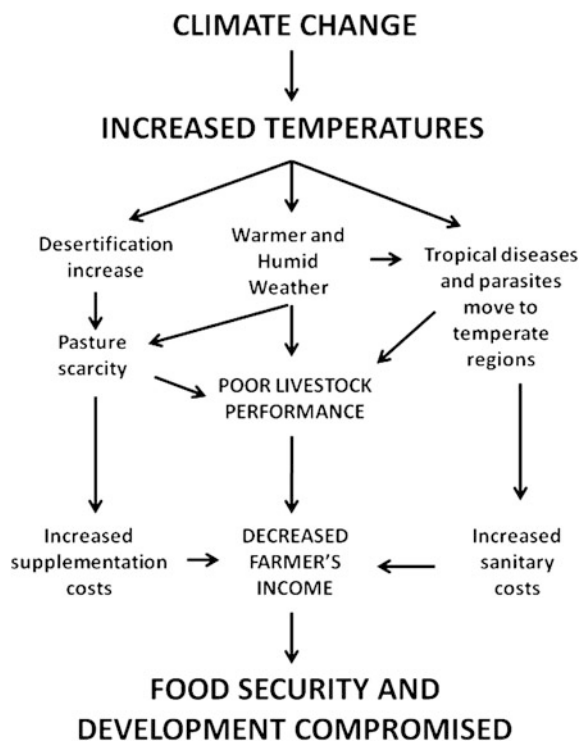


Union Republics of Central Asia gained importance in the pelt production industry, particularly in Southern Africa, although it has lost the importance of the sixties and seventies (Almeida [2011b](#)).

Fat tailed sheep anatomy and morphological characteristics have been thoroughly reviewed by Pourlis ([2011](#)). Briefly, fat tailed sheep are characterized by a deposition of fat at the level of the hind quarters. The shape and size of the fat tail varies considerably among breeds and populations. Some of the fat tailed sheep breeds have fat accumulations in other parts of the body also, such as the rump or, less frequently, the back of the neck. Fat tailed sheep usually shed their hair, characterized as being sheep with a thicker coat in the cooler months and of varied color (Lundie [2011](#)). Adults are tall and slender and tend to have long legs. Fat tailed sheep are particularly adapted to dry climates with long and persistent dry seasons. In fact, adipose tissues accumulating in the tail fat are readily mobilized in case of prolonged periods of food scarcity and correspondingly tend to decrease its size during seasonal periods of weight loss. The uneven distribution of body fat in the fat tail have a similar thermoregulatory effects as proposed for the previously described Zebu hump, as an appendage favoring heat dissipation. The tall and slender “low volume” types of bodies of fat tailed sheep are also important adaptations to periods of heat stress characteristic of dry climates. These traits, in conjunction with the longer legs, are particularly suitable for traveling long distances in search of pasture, water, and the nomadic lifestyles of herders inhabiting most dry regions of the globe. Additionally, fat tailed sheep are considered to be more tolerant to diseases and parasites, and have gregarious and defensive instincts enabling them to defend the flock from predators like jackals or foxes. These traits make fat tailed sheep the ideal group of breeds for extensive production systems in desert or semi-desert areas of the world, where they play a very important role in food security supplying milk, meat, fat, hides, and fibers for local fabrics and garments, dung for fertilizing or energy source in addition to social role as cash reserve, wealth, and status indicators (Udo and Budisatria [2011](#)).

Climate change and global warming are the major concern that will define livestock production systems and livestock productivity globally and will have even greater influence on selection of livestock types and breeds in the coming

**Fig. 2.3** Schematic view of the expected outcome of climate change as a consequence of global warming on farm animal productivity and food security



decades (Miraglia et al. 2009), particularly on disease trends in tropical regions of Africa (Van den Bossche and Coetzer 2008), Asia (Forman et al. 2008), Australia (Black et al. 2008), and South America (Pinto et al. 2008). Climate change will be discussed in detail in other chapters of this book, so are addressed here briefly. A general picture of the effects of the predicted effects of climate change on farm animal production is presented in Fig. 2.3.

Though without controversy, scientists expect global increase in atmospheric temperature particularly around Polar Regions, which would be anticipated to result in significant alterations in rain patterns and frequencies (Miraglia et al. 2009). Consequently, it is likely that present day's temperate regions will suffer changes towards becoming somehow similar to present day's tropical or dry climates. This would be associated with an increase in desertification, particularly in the tropics. Additionally, it is speculated that vast areas in Siberia and Canada may soon be adequate for agricultural and animal production purposes. The advance of tropical and dry climates toward higher latitudes will surely have adverse effects on livestock productivity, requiring significant effort from breeders and producers in order to increase adaptability. It is likely that the modern production animals, such as cattle will have to adapt in the future. Such changes will likely require smaller heat tolerant animals, able to survive hot weather and long dry periods with limited feed and water resources. Another aspect of influence of global

warming and climate change on livestock productivity is the likely increase in incidence of tropical diseases and parasitism in temperate and Mediterranean climates. The occurrence of bluetongue in Southern Europe (Barros et al. 2007) and sporadic cases in the UK (Szmaragd et al. 2010) that requires specific control measures is frequently presented as an example of disease outbreaks related to climate change. It may therefore be inferred that cattle production in temperate climates will also shift toward genotypes with higher tolerance to diseases and parasites, with particular relevance to tick-borne diseases.

### **2.3 Diseases and Parasites: Influence on Livestock Productivity**

Diseases and parasites are among the most severe factors that impact livestock production and productivity. Animal diseases have great impact on food supplies, trade and commerce, and human health globally. The last few decades have seen a general reduction in the burden of livestock diseases. Such reduction is the direct result of the availability and effectiveness of drugs and vaccines, as well as improvements in diagnostic technologies (Pearson 2006; Thornton 2010). Future disease trends are likely to be effectively managed by disease surveillance and control technologies. At the same time, new diseases have emerged and will continue to spread by the international movement of animals and animal products, such as avian influenza H5N1. This disease has caused considerable global concern about the potential for a change in host species from poultry to man and an emerging global pandemic of human influenza (Murray 2006; Thornton 2010).

From the point of view of producers, livestock diseases are essentially an economic problem. Diseases that reduce production, productivity, and profitability are associated with the cost of their treatment, disruption of local markets, international trade, and exacerbate poverty on rural, local, and regional communities. At the biological level, pathogens compete for the productive potential of animals and reduce the share that can be captured for human purposes (FAO 2009; Rushton 2009).

Livestock diseases can cause direct losses (deaths, stunting, reduced fertility, and changes in herd structure) and indirect losses (additional costs for drugs and vaccines, added labor costs and profit losses due to denied access to better markets and use of suboptimal production technology) in revenue (Rushton 2009).

Large ruminants are generally regarded as the most important domestic livestock species in the world. The importance is demonstrated by the list of products they provide. In developed countries, their contributions are mainly restricted to commercial products such as meat and milk. In developing countries they are a source of food, particularly protein for human diets, and they provide income, employment, transport, can serve as a store of wealth, and provide draft power and organic fertilizer for crop production (Perry et al. 2005; Rushton 2009). The optimization of animal production in these regions is therefore of paramount importance.



Many diseases affect livestock productivity. The added complication is that they can also cause disease in humans, such as *Trypanosomiasis*, *Salmonellosis*, and *Brucellosis*. Many animal diseases are not zoonotic, however they result in severe economic hardship (Rushton 2009). In Africa there are several tropical parasitic livestock diseases such as the tsetse-transmitted *Trypanosomiasis*, with a sub continental scale of distribution that poses a major burden on cattle farming and rural livelihoods. Increased production costs associated to *Trypanosomiasis* is expected to be compensated by reduction in productivity losses, but this may not be the case if animal healthcare services are of poor quality and the treatment is not applied correctly. This is a serious problem in many developing countries, where veterinary services are scarce. Livestock in developing countries is exposed to a range of diseases that affect productivity; it is a serious hurdle when it infects draft animals during the plowing season, limiting their ability to work. This reduces farmers' incomes from renting out draft animals and causes a reduction in the area of land that can be planted with staple food crops. Similarly, *Salmonellosis* and *Brucellosis* have also a detrimental effect of animal production.

The selected diseases subsequently described are those that in our opinion present significant economic impacts on animal production in developed and developing countries with recurring consequences. These consequences will be briefly described in the following paragraphs. In later section, we will address specific case studies on how some diseases and parasites impact livestock productivity. We will also refer to how specific animal breeds have developed mechanisms of adaptations to those diseases and parasites.

**Foot-and-mouth disease (FMD)** is a highly contagious, clinically acute, vesiculating viral disease of cloven-hoofed animals like domesticated ruminants, pigs, and more than 70 wildlife species. FMD virus is a non-enveloped icosahedral virus, member of the Picornaviridae family that contains RNA of around 8.4 kb (Alexandersen et al. 2003; NRC 2005). The most common mechanism of spread is by direct contact, ingestion, or inhalation of the virus from contagious animals or innate objects, such as contaminated vehicles, clothing, feed, or water (Alexandersen et al. 2003; NRC 2005). The disease is characterized by fever and blister-like lesions followed by erosions on the gastrointestinal tracts, the teats, and between the skin areas of the hooves (NRC 2005). FMD often leaves affected animals debilitated and livestock herds experience severe losses in production of meat and milk (Kitching et al. 2007; NRC 2005). The main effects of FMD on animal production are abortions, reduction in milk yields (increases the probability of mastitis due to damage to the teats), lameness in animals, weight loss (animals are unable to eat), and increases mortality in young animals (NRC 2005). These losses are most pronounced in intensive cattle and pig production systems. This disease is also a major constraint to international trade in live animals and their products because it cannot take place between a FMD-infected country and FMD-free country. The presence of FMD can also affect the export of fresh fruit and vegetables to FMD-free countries (Rushton 2009). In much of Africa and Asia, FMD is endemic and remains a perpetual obstacle to the export of meat and other livestock products.

**Salmonellosis** is one of the most commonly reported zoonotic diseases in humans in Europe (Kangas et al. 2007). *Salmonella* is not one disease or one causal agent. More than 2,300 serovars of *Salmonella enterica* have been identified and classified (Heithoff et al. 2008). While chickens can acquire *Salmonella* from the poultry house environment, feed, rodents, or insects or through direct contact between infected and uninfected birds (horizontal transmission), many *Salmonella* serotypes are egg transmitted (Dorea et al. 2010). Clinical manifestations of human and animal *Salmonellosis* range from self-limiting gastroenteritis to severe bacteremia and typhoid fever (Heithoff et al. 2008). The production losses or problems due to *Salmonella* go from abortions in large and small ruminants to diarrhea-associated morbidity and mortality of young animals of large and small ruminants and pigs, loss of young chicks, lower egg production by hens and turkeys, depending upon the causative agent (*Salmonella pullorum* and *Salmonella gallinarum* in hens and *Salmonella arizona* in turkeys) and adult mortality. These disease problems have many associated costs such as the treatment of sick animals, destocking of farms and higher feed costs due to poor feed conversion (Rushton 2009) that are all well described. To prevent foodborne *Salmonellosis*, various control strategies have been designed in different countries, namely eradication campaigns at farm level, improved food processing and education campaigns for households (Rushton 2009).

**Brucellosis** is one of the most important bacterial zoonoses worldwide and in particular in developing countries where this disease may have important economic, veterinary, and public health consequences. It is caused by *Brucellae* (Gram-negative, facultative intracellular bacteria) and it affects humans, large and small ruminants, and pigs. The main pathogenic species worldwide are *Brucellae abortus*, responsible for bovine brucellosis; *Brucellae melitensis*, the main etiologic agent of ovine and caprine brucellosis; and *Brucellae suis*, responsible for swine brucellosis. The disease can be spread from livestock to humans (that show similar symptoms such as abortions) via the consumption of untreated milk or milk products or by direct contact with diseased animals (Abdoel et al. 2008; Godfroid et al. 2010; NRC 2005). It is an important reproductive disease causing abortions in the later stages of pregnancy. The main losses are abortions, loss of milk production, and weak calves. This disease has high costs related with its control, such as costs with diagnostic tests, vaccination, the slaughter of positive animals, and incentives to encourage farmers to eradicate brucellosis at herd level (Rushton 2009). Brucellosis in cattle is effectively controlled and in many industrialized or developed countries eradicated. The disease in small ruminants has a considerable public health risk due to the production of soft cheeses from unpasteurized milk. Brucellosis in pigs also carries a public health risk and causes losses in production (Rushton 2009).

**Trypanosomiasis** is a disease that affects a range of species and its impact is different in different regions of the world. This disease is caused by parasitic protozoa of the genus *Trypanosoma*. In Africa, trypanosomes are mainly transmitted by the tsetse fly of the *Glossina* species. The disease is caused by *Trypanosoma congolense*, *Trypanosoma brucei brucei*, and *Trypanosoma vivax*

(Courtin et al. 2008; Naessens 2006; NRC 2005). The main interest in this disease has been Africa, which has all the trypanosome protozoas, including the trypanosomes that cause sleeping sickness. The more common symptoms for animal *Trypanosomiasis* are hyperthermia, anemia, rapid weight loss, mucous pallor, miscarriage, ‘petering out’, pica, splenomegaly, cachexia, and death (Courtin et al. 2008). Trypanosomiasis in Africa accounts for heavy losses due to mortality and morbidity in cattle and other species. Public health issues as cattle can harbor the trypanosome that causes sleeping sickness in humans and can also move it from one place to another is also a preeminent issue (Rushton 2009).

**East Coast fever (ECF)** is a disease caused by a tick-borne intracellular protozoan parasite (*Theileria parva*) transmitted by *Rhipicephalus appendiculatus* ticks. It infects T and B lymphocytes of cattle. The disease is prevalent in eastern, central, and southern Africa and has a high mortality and morbidity rate in cattle (Cicek et al. 2009; Geysen et al. 1999; Katzer et al. 2010; Rushton 2009). Efforts to control ECF are largely based on the use of acaricides to control tick population, but this approach is increasingly being compromised by the emergence of acaricide resistance in the vector tick populations. Although drugs are available to treat the disease, they are expensive and require an early diagnosis to be effective (Katzer et al. 2010).

**Bluetongue** is a non-contagious hemorrhagic disease of small ruminants and pigs caused by an arbovirus transmitted via *Culicoides* species of biting midges (Noad and Roy 2009; NRC 2005; Willgert et al. 2011). Clinical signs and lesions include cell injury and necrosis, consumptive coagulopathy (white-tailed deer), pulmonary edema, and vascular thrombosis (MacLachlan 2004). In many countries, it is present without clinical outbreaks but these may occur when climate changes encourage insect vectors of the disease to move to regions outside their original distribution. It is endemic in many tropical regions of the world and clinical symptoms are rare in indigenous animals, but are problems for the introduction of exotic animals. Therefore, this disease has a considerable economic impact in terms of restricting trade of live animals and adoption of exotic animals in countries which have endemic bluetongue. It presents minor losses in endemic areas due to reproductive problems and mortality in situations where clinical symptoms occur (Rushton 2009).

Many different agents and factors can cause diseases of livestock. Animal disease agents can have a major impact on livestock health and production and the zoonotic agents can also cause human as well as animal diseases. New, more cost-effective approaches for delivering animal health services are critical to poverty reduction processes, such as vaccines, which are critical technologies for the prevention of infectious diseases. Many animal diseases prevalent in the developing world do not occur in the developed countries. Of particular importance are the tsetse-transmitted trypanosomiasis and the tick-borne East Coast Fever in Africa, for which safe and effective vaccines do not exist. These are complicated infections, but because their distributions are restricted to developing countries and the risk of their spreading beyond Africa is minimal, the research investment on

these diseases has been very limited. However, for tropical diseases there has been some development in the study of adapted breeds to some of these diseases, so as to diminish the costs related to prevention and treatment and also to search alternatives to existing drugs.

### ***2.3.1 Diseases and Parasites: Influence on Livestock Productivity: Case Studies of Adaptation***

Adaptability of an animal can be defined as the ability to survive and reproduce within a defined environment or the degree to which an organism, population or species can remain/become adapted to a wide range of environments by physiological or genetic means (Mirkena et al. 2010).

In livestock, genetic diversity with respect to disease resistance is important given that disease-causing organisms evolve continuously and develop resistance to drugs. Today, modern livestock production is highly dependent upon the use of antimicrobial compounds and antihelmintics to control diseases and parasites. Natural resistance to diseases and parasites is not usually selected while breeding animals (Gillespie and Flanders 2010). If a new disease occurs in a country, animals with a narrow genetic base may all be affected whereas in genetically diverse livestock, the chances that some animals survive, when others die, increase (Mirkena et al. 2010). Approximately one billion cattle, most of which are in the tropics, are at risk from various tick species, tick-borne diseases and worms, all of which can cause significant production losses (Frisch 1999). Some native livestock are less affected by these challenges than imported ones. In tsetse fly infested areas of Africa, indigenous cattle have developed tolerance to Trypanosomiasis disorders, whereas those imported from non-endemic areas die if not managed appropriately and treated with chemicals. Similarly, local cattle, sheep and goats in West Africa are resistant to heartwater, a deadly disease for imported animals or crossbreds (Mirkena et al. 2010). Cattle are dipped in dip tanks or directly sprayed with acaricides to prevent deaths due to anemia, to minimize losses in bodyweight due to infestation and to protect against tick-borne diseases (Jonsson 2006).

To control ticks, strategic programs have been recommended based on applications of acaricides in spring when the number of ticks on cattle is low and the proportion of ticks in the parasitic phase is high. This results in a strong effect on the size of subsequent generations (Jonsson 2006). However, acaricide use has produced acaricide resistant ticks, leading to a continuing need for the development of new drugs. All of these strategies are not cost effective. So, a search for alternative methods of control was needed, taking into account public concerns over the safety of chemical residues in livestock products and the undesirable effects of these chemicals in the general environment (Frisch 1999).

For ticks, an existent efficacious antigen, Bm86, is the basis of two commercial vaccines, directed against the cattle tick *Rhipicephalus (Boophilus) microplus* (Hope et al. 2010). These vaccines have so far proven to be the most effective

alternative control method for spread of ticks in cattle. However, an integrated approach utilizing vaccination and high host resistance will be more cost effective in controlling ticks than vaccination alone, particularly in extensive pastoral systems (Frisch 1999).

The main method of *Boophilus microplus* control is the use of tick-resistant *B. indicus* breeds (Frisch 1999). *B. indicus* breeds have evolved a relatively stable relationship with ticks and, except in unusual circumstances, are not greatly affected by continuous exposure to ticks. However, almost all of the resistance found in different breeds is the result of natural, not deliberate selection. Nevertheless, due to low productivity of these breeds, their population size is slowly decreasing mostly due to crossbreeding with exotic breeds for increased production (Wambura et al. 1998). The resistance of the crossbreed is, however, directly related to the proportion of resistant breed in the cross. Thus, in tick-infested regions, crossing between “resistant” tropical breeds and “susceptible” temperate breeds will culminate in the need to use other control methods if production losses are to be minimized (Frisch 1999). Disease resistance is arguably one of the important traits possessed by these indigenous breeds and is an important attribute of livestock in low-input livestock production systems. Such traits, if identified, are useful in breed improvement programs involving crossbreeding of productive exotic breeds with indigenous breeds (Jonsson 2006).

**Trypanotolerance** is the capacity of certain West-African, *B. taurus* breeds of cattle to remain productive and gain weight after trypanosome infection (Naessens 2006). This infection is caused by parasitic protozoa of the genus *Trypanosoma*. In Africa, trypanosomes are mainly transmitted by the tsetse flies of the *Glossina* species. The disease is caused by *T. congolense*, *T. b. brucei*, and *T. vivax* and occurs in 37 countries resulting in a risk to approximately 60 million cattle living over 7–9 million km<sup>2</sup>. It is estimated livestock producers and consumers lose \$1.34 billion annually to trypanosomiasis in Africa. The main economic losses attributed to animal trypanosomes are related to cattle mortality and morbidity, diagnosis and treatment costs, the reduction in meat and milk production by the infected animals, and the reduction of livestock production areas. Human African trypanosomiasis, or sleeping sickness, a disease caused by *Trypanosoma brucei gambiense* and *Trypanosoma brucei rhodesiense* parasites, remains a major public health problem and occurs in 36 countries of sub-Saharan Africa. Cattle are an epidemiologically important reservoir for the human-infective parasite *T. b. rhodesiense* (Courtin et al. 2008; Delespaux et al. 2008; Naessens 2006).

African trypanosomes are unique for being able to multiply and survive in the blood of their mammalian hosts. Trypanosomes elude antibody attack by sporadically varying their surface glycoprotein, forcing the host to mount a new cycle of antibody production each time a new variant appears. In this way, the parasite manages to survive and increase its chances of transmission by tsetse or biting flies. Unfortunately for the host, the disease often leads to fatal outcomes (Naessens 2006).

Trypanosomiasis is controlled either by controlling the vector (tsetse fly) or by controlling the parasite, or a combination of both. Over the years, a large arsenal of

vector-control tools has been developed with eventual impacts ranging from reduction of tsetse fly populations to total eradication. Targets and traps, and use of insecticides on animals have been effective in controlling tsetse fly populations locally and have been used extensively in agricultural settings (Aksoy 2003; Delespaux et al. 2008).

Nevertheless, the control of animal trypanosomiasis in poor rural communities will continue to rely on the use of trypanocidal drugs. This is not surprising considering the private nature of such treatments and the difficulties in controlling tsetse flies (Delespaux et al. 2008).

An alternative approach with extensive coverage is the sterile insect technique (SIT) which has been successfully applied in the control of several important pests such as the screwworm fly and the Mediterranean fruit fly. SIT is a genetic population suppression approach and involves sustained, systematic releases of irradiated sterile male insects among the wild population. Males are sterilized by irradiation and then taken to the selected area and released. As females only mate once, by continually releasing sterile males in large numbers, the reproductive capacity of the target population is progressively reduced until the population is eliminated. However, this technique involves high costs associated with its implementation. Despite this counterpart, a recent successful eradication of *Glossina austeni* from the island of Zanzibar by SIT has demonstrated the feasibility and applicability of this technology in integrated tsetse control programs (Aksoy 2003; Vreysen et al. 2000).

The decreasing efficacy of available trypanocidal drugs and the difficulties of sustaining tsetse control increase the imperative need to enhance trypanotolerance through selective breeding, either within breeds or through cross-breeding (d'Ieteren, 1998). Trypanotolerance occurs in some African bovine breeds (*B. taurus*) such as longhorn (N'Dama) and shorthorn (Baoule or West-African Shorthorn) cattle. They have the ability to control the development of the disease, unlike zebu and exotic taurine breeds. *B. taurus* breeds are tolerant to both *T. vivax* and *T. congolense*, with a higher degree of resistance to *T. vivax*. These breeds have a relatively high capability to reduce parasitaemia waves and related anemia which are the main pathogenic effects. They also have lower mortality, superior weight gain and better reproductive performance than more susceptible *B. indicus* breeds (Courtin et al. 2008; Naessens 2006).

**Resistance to infections with endoparasites** is defined as the initiation and maintenance of responses provoked in the host to suppress the establishment of parasites and/or eliminate parasite burdens (Baker and Gray 2004). Ruminant diseases caused by gastrointestinal nematode parasite infections are the diseases with the greatest impact on animal health and productivity. Ovine hemonchosis is an endemic helminth disease of considerable economic importance in tropical and sub-tropical regions of the world. Production losses result from depression in food intake, increase in the loss of endogenous proteins, reduced efficiency of use of food energy for tissue deposition, and impairment of bone growth in sheep (Bishop and Morris 2007; Mugambi et al. 1997; Van Houtert and Sykes 1996). Due to a growing antihelminthic resistance, there is a need to find alternative and sustainable

control strategies (Magona et al. 2011). Most of the breeds identified as being relatively resistant are indigenous. This might reflect the fact that these breeds have been under natural selection for resistance for many centuries with no anti-helminthic treatment (Baker and Gray 2004). Sheep breeds resistant and/or resilient to endoparasites (predominantly *Haemonchus contortus*) include the East African Red Maasai, the Florida Native and Gulf Native in the USA, Barbados blackbelly and the St. Croix from the Caribbean. The Indonesian Thin Tail sheep have been shown to be resistant to the liver fluke *Fasciola gigantica*. The Small East African goat in Kenya and the Alpine goat in France can be included in the endoparasites-resistant goat breeds (Baker and Gray 2004).

It is generally hypothesized that differences in host resistance relates to selection for a better immune response against gastrointestinal nematodes, which affect different stages of the parasite's life cycle (Hoste and Torres-Acosta 2011). The major histocompatibility complex has been implicated as a determinant of host resistance and/or sensitivity to gastrointestinal parasitism in several species. Mucosal humoral responses to parasites have been involved in mechanisms that restrict parasite growth and mediate the expulsion of worms (Lee et al. 2011).

**Mastitis resistance** Mastitis is a complex disease which can be defined as an inflammation of the mammary gland resulting from the introduction and multiplication of pathogenic microorganisms in the mammary gland (Heringstad et al. 2000).

Mastitis causes major economic losses through reduction in milk yield and waste because milk from infected cows is unfit for consumption. Mastitis is a major cause of premature culling and it is the most common reason for antibiotic use in lactating dairy cattle. The prevention and treatment of mastitis present a serious hurdle to producers and it is always the primary concern of the dairy industry (Heringstad et al. 2000; Rainard and Riollot 2006). Vaccination against mastitis has long been an active field of research, but for the time being, the panoply of mastitis vaccines is neither well stocked nor very efficient (Rainard and Riollot 2006). Another approach to the control of mastitis is the selection of more resistant animals. Genetic improvement of mastitis resistance may reduce the need for treatment and, consequently, reduce the use of antibiotics with concomitant reduction in chemical residues in dairy products (Heringstad et al. 2000; Rainard and Riollot 2006).

Breeding for increased resistance to mastitis can be performed by direct selection corresponding to the diagnosis of infection (bacteriology, observation of clinical cases), by indirect selection using traits genetically correlated to mastitis or by a combination of both. The most commonly used indirect measures have so far been focused on milk somatic cell counts (SCC) to predict the bacterial status of udders (Heringstad et al. 2000; Rupp and Boichard 2003). Increase in milk SCC mainly corresponds to an afflux of white blood cells that come from the bloodstream into the milk to fight infection in the udder. Therefore, SCC is closely related to the magnitude of the inflammatory process (Rupp and Boichard 2003).

Scandinavian countries were the first to consider udder health in their breeding objectives for dairy cattle. In the last decade, many other countries similarly



modified their breeding objectives for dairy cattle and sheep in response to the increasing consumer's concern for better animal health and food quality, and also to maximize profitability by reducing production costs (Rupp and Boichard 2007).

Marked differences between breeds may also be found regarding tolerance to mastitis. Dairy breeds originating from eastern France (*Montbéliarde*, *Abondance*) or central Europe (*Simmentaler*, Brown Swiss) have lower SCC and clinical mastitis frequency than Holstein. Within breed, genetic variability is quite large (Rupp and Boichard 2003). Based on progress in understanding genetic basis of host's defense mechanisms, new phenotypes and genes may emerge to target key components of resistance of the udder gland, and potentially control resistance to various pathogens and environment-pathogen interactions (Rupp and Boichard 2007).

Considerable work has been made in the last decade in understanding immune mechanisms and identifying genes that play key role in the mammary gland defenses, but the function is highly complex and is still a large field for investigation. Studies combining different field approaches (genetics, QTL characterizations, immunology), including technology such as transcriptomics and proteomics, may be promising to better understand genetic basis of udder health, to predict long-term responses to selection, and to develop new tools and strategies for genetic improvement of udder health (Rupp and Boichard 2007).

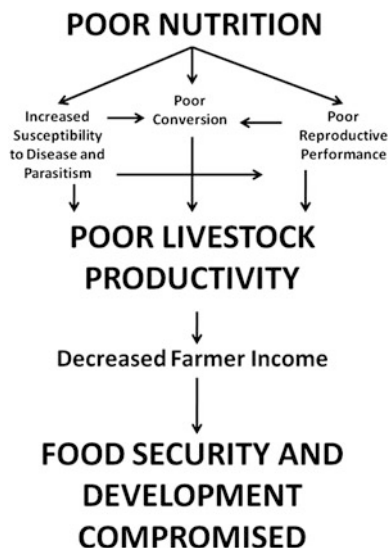
Innate immunity is a target of choice for selection against infectious diseases. Natural resistance to a number of vectors and vector-borne microorganisms exists in ruminants and varies with breed. Thus, breeding schemes based on these characteristics are encouraged since they can contribute to a reduction in the use of chemicals, to an increase in the effectiveness of drugs (as naturally resistant animals respond better to treatment), to a reduction in the risk and incidence of drug-resistant strains of pathogens and vectors and lower the cost of animal production through a diminished pathological impact, and, consequently a reduced use of drugs.

## **2.4 Nutritional Influences on Livestock Productivity: The Problem of SWL**

As discussed earlier, the rain pattern during the year strongly conditions livestock production systems through pasture development and disease and parasites outbreaks, therefore influencing animal production systems, productivity. Tropical and Mediterranean climates are characterized by the existence of a season of varied duration, when rainfall is scanty or non-prevalent. Such season is termed dry season in the tropics and summer in Mediterranean climates. During rainy season pastures are available in higher quantities and show good nutritional quality whereas dry season's pastures have poor nutritional quality with high fiber and low protein contents (Butterworth 1984), which often results in SWL. A schematic representation of the effects of SWL on animal productivity is presented in Fig. 2.4.



**Fig. 2.4** Schematic representation of the effects of poor nutrition caused by SWL on farm animal productivity and food security



To mitigate this problem, animal production systems in these regions resort to strategies such as transhumance in pastoral societies or to supplementation in developed countries. Animals that evolved in such production systems tend to have physiological adaptations that enable them to cope with SWL. In this section we discuss the deleterious effect of SWL and strategies for mitigating it to enhance livestock productivity. Such strategies rely essentially on transhumance or cattle and human population migrations, supplementation with concentrates and minerals and determining the physiological adaptations to nutritional stress displayed by farm animal breeds that were selected in regions where SWL is a severe problem.

In tropical countries, lack of feed supplementation during the dry season is frequent in extensive or traditional management systems. This situation leads to a problem of SWL of approximately 20–40% of the body weight at the onset of the dry season. This fact has been reported by several authors (Preston and Leng 1987; Clariget et al. 1998). Hence, pasture shortage significantly affects animal production in tropical nations such as Mali (Wilson 1987), Brazil (Abdalla et al. 1999), the Philippines (Alejandrino et al. 1999), South Africa (Luswati 2000; Almeida et al. 2006a, 2007), or Guinea-Bissau (de Almeida and Cardoso 2008a, b). SWL has therefore great impact on all aspects of animal production. The productive and physiological impact of SWL has been a major area of research activities for our research group over the last 12 years in laboratory and farm animals.

Our research group has studied production standards and productivity on one of the most important goat breeds of the world, the Boer goat. The results obtained from these studies clearly illustrate the deleterious effect of SWL at the level of growth, carcass characteristics (Almeida et al. 2006a), carcass minerals (Almeida et al. 2006b) several reproduction indicators in the male goat (Almeida

et al. 2007), with strong implications at the level of serum free amino acids, muscle protein (Almeida et al. 2004), and lipid profiles (van Harten et al. 2003). Subsequently, studies on the effect of SWL were directed toward experiments using two rabbit (*Oryctolagus cuniculus*) breeds with different level of tolerance to SWL. Studies were conducted to examine the male reproduction (Carvalho et al. 2009), liver regulatory enzymes (van Harten and Cardoso 2010), and the skeletal muscle proteome (Almeida et al. 2010a) levels. Similar studies were also conducted on different sheep breeds (*Ovis aries*) with different levels of tolerance to SWL. These studies included, growth (Kilminster et al. 2008) and meat characteristics (Scanlon et al. 2008), as well as proteomic studies at the liver level (Almeida et al. 2010b). In this section, we will illustrate the influence of SWL on livestock productivity using these set of interesting study cases.

SWL is a major concern in tropical, Mediterranean, and dry climates. In Southern Africa, SWL is particularly limiting due to the constraints of being a developing region with vast and remote territories. In order to study the effects of SWL at the productive level, we conducted an experiment on Boer goat bucks, indigenous to South Africa (Almeida et al. 2006a). Briefly, animals were subjected to an experimentally induced SWL for a period of 30 days. SWL was induced by feeding the animals with *Themeda trianda* (red grass) chopped from a natural pasture in South Africa in the middle of the dry season. This is an extraordinarily poor fodder, low in crude protein and high in crude fiber. Animals subjected to nutritional stress were compared to control animals that were fed the same diet supplemented with maize, molasses, and urea. Body weights and feed consumed were recorded. Animals were slaughtered and carcass traits (weight and percentages of selected carcass cuts) and the carcass chemical composition determined. As expected, animals feed with fodder supplemented with maize, molasses, and urea showed a higher live weight than animals fed with *T. trianda* alone. Carcass cuts from underfed animals represented a higher percentage of the total carcass, especially carcass cuts where muscle depots are higher in proportion to fat and bone (legs, best end chops, and prime cuts). There is an attempt by animals that were not fed with supplement to preserve the body's nitrogen reserves under prolonged nutritional stress conditions. This study clearly stressed the necessity of supplementary feeding of small ruminants fed winter veld hay, especially if the animals are to be used in subsequent breeding seasons. This study quantified for the first time the effect of weight loss on the productive performance of the Boer meat producing goats, particularly at the level of the meat production. In parallel, we evaluated the effect of SWL on reproduction by measuring scrotal, testicular, and semen characteristics in the same Boer goat bucks (Almeida et al. 2007). Results indicate negative impacts of SWL on characteristics such as sperm cell abnormalities (43% in the non-supplemented group versus 24% in supplemented group), testicular volume (35% reduction as a consequence of SWL) or scrotal circumference (35% reduction as a consequence of SWL). It is essential to supplement the nutrition of small ruminants during dry season to maintain scrotal, testicular, and semen characteristics, especially if the animals are to be subsequently used as sires.

The effects of SWL on the productive and reproductive performances of Boer goat bucks led us to investigate other aspects of nutritional impacts on Boer goats. Particular emphasis was given to physiological aspects, serum amino acids, myofibrillar protein profiles (Almeida et al. 2004) and the profiles of free fatty acids and of triacylglycerols incorporated fatty acids (van Harten et al. 2003). Regarding nitrogen metabolism profiles (Almeida et al. 2004), the aim of the work was to determine serum free amino acid and myofibrillar protein profiles in Boer goats following undernutrition in order to study the physiological consequences of undernutrition in this goat breed. Blood was collected weekly for the determination of the serum free amino acid profiles. Semimembranosus muscle was sampled for myofibrillar protein profile determinations. Following 29 days of sample collection, normally fed animals had higher concentrations of the amino acids Alanine, Tyrosine, and Citruline, while animals subjected to SWL showed higher concentration of Valine, Isoleucine, Leucine, Threonine, Methionine, Lysine, Taurine, Ornithine, Hydroxyproline, and 3-methyl histidine (Me3His), while Glycine, Serine, Aspartate, Glutamate, Arginine, Histidine, and Proline were similar in both diets. The control group showed myofibrillar protein degradation of protein C and  $\alpha$ -actinin. From the results it can be concluded that serum amino acid and myofibrillar protein profiles in the goat are strongly affected by weight loss. Amino acid results suggest that degradation of small carbon chain amino acid has a higher efficiency than degradation of long carbon chain amino acid which may have implications in directed supplementation practices as well as at the level of physiology studies that may be used to ascertain breed tolerance and adaptation to nutritional stress. Myofibrillar protein profiles suggest a disruption of muscle structure at the level of the second third of each half of the A band (protein C) and the matrix of the Z line ( $\alpha$ -actinin). Regarding the lipid profiling (van Harten et al. 2003), the aim of the study was to determine free fatty acids profiles of muscle and plasma of underfed Boer goat bucks and Boer goats fed with supplemented feed. The content of blood and muscle free fatty acids was studied. Results indicate that C16:0 as free fatty acid in the plasma suffered a significant effect of undernutrition (increase) and C18:1 showed a relative decrease in muscle fatty acid incorporated in triacylglycerols in underfed goats. C18:2 revealed a relative increase in muscle fatty acid incorporated in triacylglycerols and a relative decrease in free fatty acid in the plasma in the restricted group.

The results of these two experiments, in conjugation with the data obtained regarding the productivity losses as a consequence of SWL directed our research efforts toward the study of the several physiological components of SWL, exploiting breed differences. The study of the metabolic changes due to food restriction, highlighting energy, and protein metabolic saving mechanisms, can be a useful approach to identify the physiological pathways relevant in breed selection and development of genetic biomarkers that could be used for the selection of breeds with metabolic pathways more capable of energy and nitrogen retention, thus increasing productivity (Almeida et al. 2010a). These mechanisms will enhance the whole process of selection and development and ultimately lead to relevant contributions to the improvement of animal husbandry. Therefore, the use

of these techniques as tools for animal selection is envisaged to be of paramount interest in the twenty-first century (Fadiel et al. 2005), mitigating the adverse effects of SWL on livestock productivity.

To study such breed differences, we started with two rabbit breeds subjected to control and food restriction conditions: wild rabbits (not selected to increased meat productivity) and the well-known meat producer New Zealand white (the most common domesticated breed). Studies focused on male reproductive performance (Carvalho et al. 2009), liver regulatory enzymes (van Harten and Cardoso 2010), and the skeletal muscle proteome (Almeida et al. 2010a). The objective of using the rabbit as a mammalian model would allow the extrapolation of the results to other conventional farm animal species such as swine, cattle, or sheep.

In these studies, a 20% weight reduction was induced in the two above-mentioned rabbit breeds: New Zealand white, a selected meat producer (*Oryctolagus cuniculus cuniculus*) and the Iberian wild rabbits (*Oryctolagus cuniculus algirus*). Regarding the proteomics experiment (Almeida et al. 2010a), the determination of the differential protein expression in the *gastrocnemius* muscle within control (ad libitum) and restricted diet experimental animal groups, using techniques of two-dimensional gel electrophoresis and mass spectrometry-based identification was carried out. Results show that spots identified as energy metabolism L-lactate dehydrogenase, adenylate kinase,  $\beta$  enolase and  $\alpha$  enolase, fructose biphosphate aldolase A, and glyceraldehyde 3-phosphate dehydrogenase enzymes are differentially expressed, in restricted diet experimental animal groups. These enzymes are available to be further tested as relevant biomarkers of weight loss and putative objects of manipulation as a selection tool toward increasing tolerance to weight loss. Similar reasoning could be applied to spots corresponding to important structural proteins tropomyosin  $\beta$  chain and troponin I. Additionally, a spot identified as mitochondrial import stimulation factor seems of capital interest as a marker of undernutrition and a possible object of further studies aiming to better understand its physiological role. In parallel, we conducted a study on the Hepatic glycolytic, lipidic, and protein regulatory enzyme activity at the transcriptional and metabolite levels (van Harten and Cardoso 2010). Insulin-like growth factor (IGF-1), triiodothyronine, and cortisol were also evaluated. In the glycolytic pathways, the New Zealand control rabbits showed a higher phosphofructokinase and pyruvate kinase activity level when compared to the wild rabbit, while the latter group showed a higher expression of glycogen synthase, although with less glycogen content. In the nitrogen metabolism, our results showed a lower activity level of glutamate dehydrogenase in Wild Rabbits when subjected to food restriction. The lipid metabolism results showed that although Wild Rabbits had a significantly higher mRNA hepatic lipase, non-esterified fatty acid levels were similar between the experimental groups. New Zealand rabbits exhibited a better glycemia control and greater energy substrate availability leading to enhanced productivities in which triiodothyronine and IGF-1 played a relevant role.

Results obtained in both studies in conjunction with the productive data led us to conduct further studies aimed at understanding breed differences in sheep as a consequence of the effect of SWL. Further trials were therefore conducted in sheep

with very diverse genetic background and varying levels of adaptation to SWL: the Australian Merino (Animals of European origin and less tolerant to SWL), the Damara, a fat tailed sheep from Southern Africa with high levels of adaptation to nutritional stress and the Dorper, a composite breed of mixed European and African origin with an intermediate level of adaptation to nutritional stress.

These studies focused essentially on both productive trials, as well as on proteomics-based comparison of the hepatic tissue exploring breed differences. Scanlon et al. (2008) and Kilminster et al. (2008) studied the effects of food restriction (15% live weight decrease) on growth and carcass characteristics of pure Damara, Dorper, and Australian Merino ram lambs. Contrary to our expectation, results indicate that food restriction affected all breeds similarly, as weight lost proportional to initial body weight (Scanlon et al. 2008). As expected, Dorper rams had higher proportions of weight gains than Damara and Merinos. In addition, it was found that differences in carcass and loin meat characteristics were seen between breeds and between feeding levels. Dorper and Damara lambs had a higher dressing percentage than Merino lambs and this might partially be explained by differences in fleece weight. Dorper lambs had heavier carcasses generally when fed to gain weight than the Damara and Merino lambs. Meat from Damara lambs was darker in color than that from other breeds, an indication of differences in metabolic rate. Feeding to lose weight reduced carcass weight and fatness but not dressing percentage. Meat from lambs fed to lose weight tended to be lighter and less red in color than meat from lambs fed to gain weight.

Additionally, we conducted experiments on the effect of SWL on liver proteome profiles in the same sheep breeds (Almeida et al. 2010b). At the end of the afore-said trial, animals were euthanized and liver sampled. Total liver protein was extracted; quantified and used in two-dimensional gel electrophoresis analysis. After gel analysis, a total of 67 spots were selected for identification using MALDI-TOF/TOF. Results obtained reflect the extreme complexity of the liver when compared to tissues previously studied on the SWL issue, particularly the skeletal muscle in two different rabbit genotypes (Almeida et al. 2010a), and also a high conservation of protein expression levels in this tissue as a consequence of weight loss. The study suggests that proteins such as glutathione S-transferase, triose phosphate isomerase, phosphoglycerate mutase, carbonic anhydrase, carbonyl reductase, and a stress protein similar to heat shock protein could be considered as biomarker for the tolerance to weight loss in sheep. To the best of our knowledge, this work was the first proteomics-based approach to the study of protein expression profiles at the liver level in underfed sheep. The study was also enriched by the possibility of comparing three different breeds of sheep that show apparent different tolerance levels to weight loss, distinct metabolism type, and breed origins.

SWL is the main constraint to animal productivity in tropical and Mediterranean regions, the results obtained in the aforementioned studies, allowed us to quantify the effects of SWL on ruminant production and productivity, primarily at an experimental level. Further studies were conducted on numerous physiological and biochemical aspects of effects of SWL and different levels of adaptation on

animals of commercial interest such as the rabbit and the sheep. These strategies will enhance animal breeding and development of effective selection tools for obtaining genotypes with higher tolerance to SWL and improved productivity.

#### ***2.4.1 Nutritional Influences on Livestock Productivity: Adaptation to Poor Quality Diets in Ruminants at the Oral Cavity Level: Browsers vs. Grazers***

In this section, we will explore the differences between ruminants consuming varied types of foliage (grass vs. shrubs; i.e., browser vs. grazers) primarily at the level of the adaptations that are found at the oral cavity. The coexistence of species in the same areas, without competing is possible due to the differentiation of ecological niches. Support for this statement concerns the ruminant feeding types proposed by Hofmann (1989): browsers or concentrate selectors, grazers, and intermediate feeders. This classification was based on the relation between the functional–anatomical and histological characteristics and the different chemical and physical properties of the respective food sources. In general, grazers have a highly developed fermentation system enabling them to digest fibrous fractions of plants with high amounts of cellulose and lignin, such as monocotyledons. On the other hand, browsers are animals that select for fresh, juicy foliage, forbs and other dicotyledonous matter, highly digestible, relatively rich in energy and protein, and low in fiber. In the between are the intermediate feeder type that behaves as browsers or grazers seasonally, according to the available vegetation species. One of the main sources of diet variation among these Hofman’s ecophysiological feeding types is the level of plant secondary metabolites (PSMs) (e.g. tannins) present in diet, which require detoxification mechanisms within consumers. Browsers are faced with diets with high levels of these compounds, followed by intermediate feeders and ultimately by grazers. Although some authors criticized (reviewed in Pérez-Barberia et al. 2005) some of Hofman’s assumptions, this continues to be a widely accepted classification scheme.

Since ruminants are faced with variable levels of nutrient and PSMs in plants, they must be able to differentiate foods with different compositions. They also need to associate the sensory properties of foods, namely palatability, with the metabolic consequences of eating them, in order to increase diet quality and maintain productivity. The role of oral cavity in food perception is extremely important in the exploratory behavior. Learned associations formed between the sensory properties of the food perceived in the oral cavity and its post-ingestion effects allow individuals to modify feeding behaviors (Green et al. 1984; Provenza 1995; Ralphs 1997). In fact, preferences are likely indicative of underlying physiological adaptations promoting further behavioral, physiological, and ultimately genetic differences between the species. For example, different ruminant

species with different tolerance levels for PSMs react differently to diet sensorial cues.

With regards to ruminant diets, the main sensorial characteristics perceived at the mouth level and responsible for the acceptance or rejection of food items are bitter taste and astringency. Glendinning (1994) hypothesized that mammals in different trophic groups have evolved different strategies for coping with the unpredictable bitterness/toxicity relationship of food items. Accordingly, bitter taste thresholds and bitter rejection response is dependent on the relative occurrence of bitter and potentially toxic compounds in a species regular diet. Lower thresholds of bitter detection would reduce drastically the chances of toxic food ingestion. However, for species which have to deal with higher levels of PSMs, which are regularly associated to these sensory characteristic, the presence of much higher bitter taste sensitivity would not be advantageous at the expense of limiting drastically the range of potential foods.

In all the physiological oral processes, saliva is central. Whole saliva constitutes the fluid that bathes the oral cavity. It originates from major and minor salivary glands and from gingival crevicular sulcus, the latter of which is an area located between teeth and marginal free gingival. This fluid has the main role of protection and maintenance of the upper part of the digestive tract, acting through lubrication, buffering action, maintenance of tooth and mucosal integrity, antibacterial and antiviral activity. Moreover, it can play several roles in feeding behavior, through taste perception and assistance in the processes of food ingestion and digestion (Mese and Matsuo 2007).

The salivary glands of ruminants, which rely on foregut fermentation for digestion, differ from other mammalian salivary glands (Steward et al. 1996). The amounts of saliva produced are extremely high as it is an important source of fluid to rumen [e.g. one sheep (*O. aries*) producing at least 15 L/day (Kay 1960)]. The ruminant parotid saliva, with a pH of 8.2, is unusually rich in mineral ions, particularly sodium, phosphate, and bicarbonate (McDougall 1948), which are involved in providing a buffered medium for ruminal fermentation. Ruminant parotid serous glands are the main facilitator in the digestive processes during feeding and rumination, whereas submandibular, sublingual, and other minor mucous salivary glands are confined to lubricate the mouth and esophagus (Carr 1984).

Mouth being the first entry level for food, saliva plays an important physiological role in protecting ruminants against external and internal milieus. Secretion and composition of saliva is mainly under autonomic nervous system control, allowing a rapid adjustment to changes in dietary conditions. The role of saliva in ruminant dietary adaptation can be viewed as a consequence of two main inter-related functions: importance of saliva in food perception and palatability, and the direct interaction between salivary proteins and PSMs, acting as a defense mechanism against negative effects of their ingestion.

Animals possessing different dietary habits concomitantly secrete different saliva volumes, buffer capacity, and protein composition (Sales Baptista et al. 2009). Browsers have been referred as having a greater secretion of thin serous



saliva, followed by intermediate feeders, being grazers the ones with the lowest volume of secretions (Hofmann 1989). Saliva protein composition varies considerably among species, and also reflects their diverse diets. Animals using identical feeding niches may exhibit similarities in their saliva protein composition, whereas the presence of particular proteins appears to be specific for particular feeding niches. In sheep and goats we observed that salivary proteins are expressed at different levels, between the species, what appears to be related to food consumption (Lamy et al. 2009). This issue will be further developed.

Salivary proteins can interact with taste substances, modulating taste perception and, indirectly, dietary habits. Although not present in saliva of ruminants, alpha amylase is a salivary protein suggested to be important in food perception. This protein initiates the digestion of starch in the mouth and this may have some influence on taste of carbohydrates (Becerra et al. 2003). Other salivary enzyme suggested to interact with food components, changing their original taste, is lingual lipase, which is secreted by the von Ebner's minor salivary glands. This protein can break down dietary triglycerides to fatty acids and other small molecules, which, in turn, can stimulate taste receptors and result in fat perception (Kawai and Fushiki 2003). Moreover, its expression levels change according to the levels of dietary fat (Armand et al. 1990). Von Ebner's gland protein, abundantly expressed in the small von Ebner's salivary glands of the tongue, was known to bind to lipophilic molecules some of which have bitter taste, influencing their perception (Gurkan and Bradley 1988). The salivary carbonic anhydrase (CA) VI has also been associated with taste sensitivity. One of the ways this protein contributes to taste function seems to be by protecting taste receptor cells (Leinonen et al. 2001). CA VI expression was recently demonstrated in both sheep and goat saliva, although our results suggest differences between the two species in the expression of some isoforms (Lamy et al. 2009). However, it is difficult to make conclusions on how this relates to species different ingestive behavior without further studies. Although not studied in ruminants, salivary cystatins are also proteins differently expressed based on diet composition, with some researchers associating them to an aversive oral stimuli such as pungency and astringency (Katsukawa et al. 2002; Dinnella et al. 2010). The involvement of salivary proteins in ruminant taste perception, however, is a very interesting subject for research that still needs to be further investigated.

Animal species may have to deal with distinct levels of PSMs present in their diet differently during the year, as these compounds vary among plants and are influenced by climatic conditions. Among the PSMs, tannins have a major importance in ruminant food choice and nutrition. Tannins are a class of PSMs with a high capacity to bind proteins, polysaccharides, carbohydrates, and other macromolecules. Tannins may form stable complexes that tend to precipitate (Lu and Bennick 1998), which can result in the anti-nutritional property usually attributed to these compounds. The levels of dietary tannins influence food selection, and may even result in food rejection attributable to either their astringent properties or detrimental post-ingestion effects (Iason 2005). High tannin levels reduce acceptability of plants by cattle, sheep, and goats



(Perevolotsky et al. 1993). There are several studies reporting salivary proteins as a countermeasure against the potential negative effects of tannins. Such countermeasure role is essentially due to the high affinity that some classes present for these PSMs, resulting in the formation of complexes, which change the way these phytochemicals are perceived in the mouth and the way they act through the digestive tract. A large number of researchers (reviewed in Shimada 2006) link the occurrence of such tannin-binding salivary proteins (TBSPs) to the levels of tannins present in the individual's regular diet: species with low tannin content in their natural forage, such as grazers, have little or none of such salivary proteins, whereas browsers having a diet rich in tannins throughout the year present TBSPs constitutively. Species in which the levels of tannins in the diet change seasonally can adapt by producing higher amounts of TBSPs only when consuming tannin-rich diets (Austin et al. 1989; Robbins et al. 1987; Fickel et al. 1998; Lamy et al. 2011).

The most studied TBSPs are the proline-rich proteins (PRPs). PRPs have a high capacity to bind tannins, and the complexes formed appear to be stable across pH ranges of the digestive tract, allowing tannins to pass intact through it and to be excreted (Bennick 2002). It was suggested that the presence of these proteins might override the negative effects of tannins on palatability, and consequently on feed intake, improving the utilization of plants containing such compounds (Glendinning 1992). Besides PRPs, other salivary proteins show affinity for tannins, are salivary histatins (Wroblewski et al. 2001), and salivary amylase (Zajácz et al. 2007; da Costa et al. 2008; Lamy et al. 2010). However, these proteins seem to be absent from ruminant saliva, and as such they do not contribute as a defense medium for these animals.

Until now, there has been some controversy about the presence of TBSPs in sheep and goat saliva. Whereas some researchers suggest that sheep and goat saliva does not have a great ability to bind tannins (Pérez-Maldonado et al. 1995), others point to the possibility of their presence in both species (Vaithianathan et al. 2001). There is more speculation about the occurrence of TBSPs in goat than in sheep. According to the “niche theory” (i.e., the relative position of a species in its ecosystem), goats produce TBSPs since their diet is based in tannin-rich browse (Kababya et al. 1998; Landau et al. 2002). Gilboa (cited by Silanikove et al. 1996) found that the parotid saliva of goats was relatively rich in proline (6.5%), glutamine (16.5%), and glycine (6.1%). This author also observed that the concentration of parotid saliva of goat fed tannin-rich diet was higher as compared to goats maintained on diets low in these PSMs. On the other hand, other researchers (e.g. Distel and Provenza 1991) did not detect TBSPs in the saliva of goats even when fed a tannin-rich diet.

In the last few years, our research has focused on studies concerning the influence of saliva in tannin-rich diet consumption by ruminants. We observed differences between the salivary proteome of sheep and goats (Lamy et al. 2008; Lamy et al. 2009). These two ruminant species, in Mediterranean areas, are frequently found together in pastures and although sharing the same areas, they do not compete, since they select plants and/or plant parts with different

characteristics, namely the levels of tannins (Gong et al. 1996). Accordingly, we suggest that the different salivary protein profile may be related to this difference in ingestive behavior. In fact, when subjected to condensed tannin-enriched diets changes in the expression profiles of some proteins were observed (Lamy et al. 2011). By using proteomic approaches, it was observed that the consumption of quebracho tannins resulted in the increase in the expression of the proteins cytoplasmic actin 1 and annexin A1, in both species. We do not know whether these proteins may act as TBSPs, or whether they are only the consequence of an increased salivary gland function induced by tannins. For example the increase of actin 1, which is a protein from the cytoskeleton, may be related to the “apocrine-like” mode of salivary secretion present in ruminants (Stolte and Ito 1996) and to a potential increased salivation rate resulting from tannin consumption. Additionally, annexin A1 is a protein already shown to be increased in humans after tasting bitter/sour substances (Neyraud et al. 2006) and a relation of this protein to sensory properties of tanniniferous foods is not to be discarded. However, to our knowledge, an association of this protein to tannin consumption has not been reported in the literature.

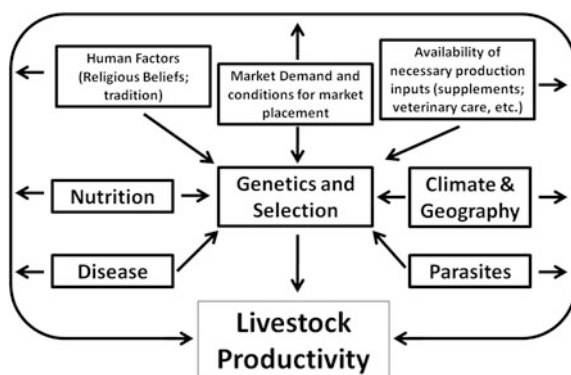
A recent study (Hanovice-Ziony et al. 2010) also failed to identify potential proteins that bind tannic acid or quebracho tannins in goat saliva. However, these researchers observed that goat mixed saliva possesses a considerable affinity to tannins. A possible (although less explored) explanation offered for this affinity of goats mixed saliva to tannins is the potential role of salivary mucins. Van Soest (1994) had reported that goats may secrete higher levels of salivary mucins than sheep or cattle, and for that reason they could be more tolerant to high levels of dietary tannins. However, these hypothesis need to be further explored, since the role of salivary mucins in astringency perception is not completely clear.

In conclusion, several reasons seem to indicate that the oral cavity characteristics, namely of saliva are important in ruminant adaptation to diet. Although in other species saliva has drawn attention in the last years, in ruminants it has been less studied. However, there are evidences pointing to the importance of thoroughly investigating ruminant saliva interaction with diet in order to better understand ruminant food choices, which may allow improvements in nutritive management and therefore on ruminant productivity.

## 2.5 Final Considerations

This chapter was an attempt to address the most significant factors affecting livestock productivity: Climate, Health, and Nutrition. We have made an effort to analyze the factors individually. In our opinion these are extremely complex factors that are difficult to quantify, particularly in extensive production systems. Nevertheless, other important factors also exist. Such factors are most of the time human influenced and include, among other aspects, livestock selection, a tool that has been in practise since the Neolithic period and that has achieved a high level of

**Fig. 2.5** Major factors influencing livestock productivity and their interconnection. Preponderant factors (nutrition, climate, diseases, and parasites) are shown with a larger font size



sophistication over the last 200 years. Other man-made factors include religion and cultural beliefs that strongly influence choices in animal production species or breeds. Finally, economical constraints, marketing choices, and access to infrastructures such as roads, harbors, and railways are also strong factors that have great impacts on livestock welfare and productivity. In Fig. 2.5, we present a schematic representation of the major conditionings of farm animal productivity.

To minimize the effect of all the above-mentioned adverse factors in farm animal productivity, it is essential to design mitigation strategies at the local, regional, national, and transnational level. In our opinion, it is vital that such strategies would focus on the study and use of local genetic resources showing a high level of adaptation to the most significant issue for that specific region, either climate, disease, or nutrition-induced. Such studies have necessarily to be directed towards the full comprehension of the local breed's genetic background and production ability, as well as the search for markers of tolerance to those limiting factors. Such markers would be of great importance and use in the definition of selection strategies and objectives to increase livestock productivity, with special reference to developing countries. Such a strong research input would allow decreasing the need for costly production factors like disease or environmental control costs, as well as feed supplementation. A similar strategy would need to be thought at the local, regional, national, and transnational level and would require significant cooperation between North and Southern countries, state and private organizations, aiming to improve the productivity of the farming systems, therefore improving farmers' incomes, standard of living and ultimately, the sustainable development of whole communities. This would be an outstanding contribution to the fulfillment of the Millennium Development Goals established by the United Nations.

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