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Review

A balanced perspective on animal welfare for improved meat and meat products

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Abstract

Increased public concern for animal welfare in the logistics chain has led to a rise in the scrutiny of the treatment of food animals. Factors affecting the status of welfare of slaughter animals begin at the farm and occur during transportation and at the abattoir. The activities that animals pass through before slaughter are thought to have negative effects on both the animal and the product. Before or during this period, animals suffer pain, which compromises their physical, health and biochemical status, and meat quality and quantity; which leads to economic losses. Environmental impact plays a role in the behaviour, growth, development and welfare of animals, even though it is associated with the production of greenhouse gases and biodiversity. Food producers are also mindful of the challenges of feeding the ever-increasing human population. Although the issues of animal production, which range from the environment to human health, have been discussed, animal welfare-related factors that are at play in the production chain of farm animals must still be addressed. An understanding of the animal's environment, behaviour and the biochemical interactions that are at play in stressful conditions; and the implications of these for animal health and welfare are key to developing effective mitigation strategies. Therefore, the objective of this review is to highlight the literature on animal welfare, and suggest strategies that could be adopted for the improvement of meat animals, meat quality and meat products.

Keywords: Avoidance behaviour, climate change, biotechnology, genetic modification, stress biomarkers, road transportation

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Introduction

Research has been conducted on the sustainability of the South African livestock sector (Meissner *et al.*, 2013), the impact of animal source products on human nutrition (Schönfeldt *et al.*, 2013), climate change and livestock production (Rust & Rust, 2013), production systems and management practices on the quality of meat products (Webb & Erasmus, 2013). Chulayo *et al.* (2012), Gajana *et al.* (2013), Stockman *et al.* (2013) and Vimiso & Muchenje (2013) emphasized that animals experience stressful conditions in transportation, which negatively affect their welfare and meat quality. Delgado (2003) and Hoffman & Cawthorn (2013) carried out research that was aimed at finding ways of increasing protein sources that would meet all needs since meat is an important constituent of the diet for many consumers.

There is increased public concern about animal welfare in the production logistic chain. Therefore such concerns require more research attention in order to avoid violations of animal rights (Grandin, 2005; Boissy *et al.*, 2007; Fraser, 2008). Animal production processes include rounding up, kraaling, loading, transporting and off-loading in the lairages at the abattoir. There is increasing awareness of the use of methods that are pain- and stress-free when handling animals (Al-Fartosi *et al.*, 2010) in such processes. For example, during transportation, high ambient temperatures, truck vibration, movement and acceleration, confinement, noise and crowding expose animals to stress, which compromises their physiological and biochemical processes, meat quality and quantity, resulting in economic losses (Bourguet *et al.*, 2011; Chulayo *et al.*, 2012; Miranda-de la Lama *et al.*, 2014). Prior to slaughter, animals experience excessive stress owing to a sudden change of environment, which increases the secretion of enzymes (creatine kinase, creatine phosphokinase, transaminases and lactate dehydrogenate) and hormones (catecholamines

and cortisol), consequently reducing the quality of meat and its products. In such instances, animal welfare is compromised, resulting in reduced meat quality and downgraded carcasses (Spores *et al.*, 2008; Muchenje *et al.*, 2009a; Rosado *et al.*, 2010; Chulayo *et al.*, 2012; 2013). This happens against a background where numerous acts, regulations and codes of conduct are in place to safeguard animals from stress and pain.

The world population of human beings is expected to reach nine billion by 2050. These people will ultimately require animal products from associated processes from the farm to the slaughter floor (UN, 2011). Food producers are also mindful and aware of the challenges associated with feeding this ever-increasing population. In spite of these challenges, animal producers are eager to adopt and apply biotechnologies that would improve the yields of crops that are utilised by livestock and human beings (Wang *et al.*, 2013a). However, there are constant animal welfare challenges in such systems. Therefore growing activist group campaigns promote a reduction in meat consumption. If consumers heeded such calls, there would be a significant environmental impact and ultimately a change in the whole agricultural sector (Capper, 2013). Schönfeldt *et al.* (2013) suggested that human health and the quality of life could be improved by choosing animal source foods that have high nutrient content. However, strategies that could be implemented to make food from stress-free animals healthier require further research. Therefore, the objective of this review is to focus on the effects of pre-slaughter stress on animal welfare and meat quality, and to discuss strategies that could be employed to improve meat quality and meat products.

Pre-slaughter stress, animal welfare and their implications for livestock production

Demand for animal-friendly products

Interest in animal welfare has been on the rise in recent years because of alleged poor treatment given to animals before slaughter. Handling affects the biochemical and physiological processes of an animal, resulting in the reduction of meat quality (Broom, 2000; Bourguet *et al.*, 2011; Chulayo *et al.*, 2013). Animal welfare incorporates behaviour, feeling, the ability of an animal to cope in different environmental conditions that are conducive to the well-being of the animal, disease control, management and humane slaughter (Al-Fartosi *et al.*, 2010; OIE, 2010). At the farm, animals go through daily, monthly and once-off routine management procedures. These routine husbandry practices include weighing, examining physical health, vaccinating, dehorning, branding and castrating. These farm management practices could be painful and stressful to animals.

Animal welfare involves investigating the relationship between animals and their physical environment, as well as their response to humans. However, there have been debates around the term 'welfare' because of different interpretations and moral assessments among cultures, regions, eras and individuals (Yeates, 2010; Ohi & Van der Staay, 2012; Probst *et al.*, 2012). Grandin (2013) stressed that there is increasing concern about the methods that are used to handle the animal and render it unconscious before slaughtering. Therefore, when defining animal welfare, moral and ethical standards of the society should be considered because of the values that are laid by that society on its animals (Webb, 2013). Some consumers still complain about poor management of animals and state that animal environments must be improved and a framework established for integration and uptake within the industries (Einsiedel, 2005; Crony & Millman, 2007). In most cases, consumers' views about animal welfare issues are rarely considered, although production must be aimed at attracting their purchasing behaviour.

Animal welfare is generally associated with producers, retailers and the industry. However, consumers are interested in knowing where and how the animals have been raised. Consumers argue that farmers may claim to take care of their animals, while they disregard the reality that product quality is the predictor of welfare-friendly buying power (Crony & Millman, 2007). However, despite consumer concerns, there is a need to conduct special programmes that integrate what to consider when shopping with what happens at the farm. This is because of the differences between rearing farm animals for improving meat and keeping pets for companionship (Freedom Food Report, 2007). Animal welfare has become a thought-provoking topic nowadays, because consumers are interested in being fully acquainted with production methods, from where the animal was raised and slaughtered until it reached the table (Velarde & Dalmau, 2012).

The demand for welfare-friendly products is significant to the potential of marketing and communicating activities that can trigger consumer attitudes towards purchasing the product. In addition, consumers' interests are crucial to consider when adopting improvement methods at the farm as this has a direct effect on their purchasing decisions (Troy & Kerry, 2010). This is associated with health, welfare and disease-resistant animals (King *et al.*, 2006; Freedom Food report, 2014). Therefore, to provide an assurance of good animal welfare and healthier foods to all participating supply chains, animal genetics has been employed to breed animals that can survive in new environments (Koknaroglu & Akunal, 2013). Scholtz *et al.* (2013) suggested that farmers ought to use genetic modification to breed animals that would adapt to the changing environment and be less susceptible to heat stress, drought and floods. According to Assan (2014), livestock producers could apply genetic modifications which promote animal fitness and adaptation,

while the environment could be modified (houses, shelters and improved drainage systems) to reduce animal losses because of climate change. In addition, Rust & Rust (2013) reported that constant research, education and sensitization are needed in order to adapt to and combat the possible effects of climate change at local, national and regional level.

Management of human-animal relationship

There is a relationship between human beings and animals that is closely linked with animal welfare freedoms (MacKay *et al.*, 2013). Among these freedoms, fear is an important factor for cattle and is known to alter behavioural response to stimuli. Fear results in stress, decreased health and reduced productivity in farm animals (EFSA, 2011). However, by definition, animal welfare is the negative or positive quality of life observed in animals, and it depends on how they feel at a particular time and place (Carenzi & Verga, 2007; Green & Mellor, 2011; Veissier *et al.*, 2012). It is related to avoidance behaviour, animal physiology, cognitive status, emotional state and animal biochemistry, as animals respond to environmental stimuli (social or physico-chemical) (OIE, 2010; Hemsworth & Coleman, 2011; Wickham *et al.*, 2012). High levels of fear in animals reduce their growth and reproductive performance. For example, pigs that were transported for longer hours with a reduced lairage period than those transported for shorter durations with increased lairage duration had increased cortisol concentration because of fear arising from transport stress (Jama, 2014). In cows, fear of humans resulted in reduced milk yield, and lower protein and fat contents (MacKay *et al.*, 2013).

Poor animal handling has been identified as having a substantial effect on the behaviour, physiology and the productivity of commercial farm animals (Williams *et al.*, 2012). Because of poor transportation, which leads to physical stress in animals, they become afraid to drink water in a novel environment such as abattoir lairages. In this environment, fear results in economic losses by reducing carcass weight, increasing bruises and high ultimate pH (pH_u), with dark firm dry (DFD) cutting beef, which is not conducive to packaging. Therefore, animal welfare conditions during herding, regrouping, loading and transporting are crucial, and must be improved in order to reduce stress and the fear response to improve animal and meat production (Werner *et al.*, 2013).

Welfare of animals during transportation

Transportation is an inevitable husbandry practice that is encountered by animals. It becomes stressful to them (Nwe *et al.*, 1996; OIE, 2010) because of the processes and activities involved, such as the creation of stress (and at times death), spread of disease, bruising, high stocking density, noise, vibration, lack of exercise, prolonged standing, environmental temperature and humidity, and feed deprivation (Vimiso & Muchenje, 2013). Long hours of transportation cause changes in the behaviour of animals, and their circulatory system and immune function, which affects the welfare of animals and meat quality negatively (Ake *et al.*, 2013). On the other hand, the genetic make-up of the animal regulates handling stress, especially when it comes to animal temperament (Dalla Costa *et al.*, 2007; Von Holleben *et al.*, 2010; Browning & Leite-Browning, 2013). Research in poultry indicated that stress responses are considered essentially adaptive and protective, because they are expected to minimize the detrimental effects of the stressor. This can be achieved by understanding the homeostatic control that is induced by transportation stress (Mitchell & Kettlewell, 1998).

Animals are exposed to heat stress in the pre-slaughter environment, especially under hot weather conditions. The mortality of animals, especially chickens and pigs, increases because of heat stress and long distance transportation without rest (Von Keyserlingk *et al.*, 2009; Melesse *et al.*, 2011). In addition, heat stress affects the metabolism and performance of animals because they become too sensitive to heat, especially if there is no air circulation during transportation (Dalla Costa *et al.*, 2007; Koknaroglu & Akunal, 2013; Zeferino *et al.*, 2013). Stress is a physiological disturbance that is linked to mental states associated with threatening or harmful and painful situations (Von Holleben *et al.*, 2010). As environmental temperatures rise beyond the animal's body temperature, the rate at which heat is dissipated by the animal decreases, causing a rapid increase in its respiratory rate (Caulfield *et al.*, 2014). Heat is initially dissipated primarily by passive mechanisms, which include radiation and convection. This situation is prevalent in live animals, whereby metabolic heat, and heat from the environment increase the animal's body temperature. Heat stress is said to be an indicator of poor animal welfare as it results in increased chances of mortality.

Heat stress results in an increase in restlessness, sweating, respiration and heart rate, rectal temperature and a decrease in the reproductive traits in animals (Melesse *et al.*, 2011). This leads to a rapid reduction of glycogen levels required for post-mortem conversion of muscles to meat. DFD beef develops in cattle ($pH > 5.9$), while in poultry and pork, a rapid fall of pH ($pH < 5.3$) results in pale soft and exudative (PSE) (Young *et al.*, 2004; Gregory, 2010; Gajana *et al.*, 2013). Elevated environmental temperatures affect poultry performance, physiology and their immune system (Star *et al.*, 2009; Melesse *et al.*, 2011), and

reduced feed intake, slaughter weight, myoglobin content and meat sensory properties in rabbits (Zeferino *et al.*, 2013), PSE pork and increased bruising score are associated with cold ambient temperatures (Dalla Costa *et al.*, 2007). There are few reports on the effect of heat stress in sheep and cattle, although Gregory (2010) stated that occurrences of cattle that were dead on arrival and incidences of DFD beef had been observed.

Animals show signs of avoidance behaviour, which leads to delayed movement (Mota-Rojas *et al.*, 2012; Strappini *et al.*, 2012). Marenčić *et al.* (2009) reported that when bulls are in the same lairage there is undue stress and hence detrimental effects to the quality of the beef. Some animals squash one another, fall or fight, while others need to be prodded to move forward. These may lead to the occurrence of bruises, which negatively affect the quality and quantity of meat. Bruises are an indication of welfare problems during road transport (Miranda-de la Lama *et al.*, 2012). Bruised tissues may store historical information about the harmful situations that the animal underwent before slaughter. It therefore becomes imperative to reduce stress effects in slaughter animals such as mixing species and sexes during transportation and at the lairages

Biochemical effects of pre-slaughter stress

Homeostatic imbalance associated with oxidative damage

Livestock animals experience extrinsic and intrinsic stress, which lead to homeostatic imbalance. This is because they undergo intense selection for specific traits, which may have negative implications on their behaviour, physiology and immunological state (Adenkola & Ayo, 2010). On the other hand, animals become more sensitive when they are exposed to novel environmental conditions (Kristensen *et al.*, 2004). The balance of homeostasis is maintained by the operation of several overlapping and complex antioxidant systems, which is a contributory factor to disease susceptibility (Caron *et al.*, 2000). Animal exposure to pathogens that reduce immunity has been observed to be determined by the interaction of the animal with its environment. Under those environmental changes, the homeostatic processes are regulated by reactive oxygen species (ROS) and reactive nitrogen species (RNS) (Falowo *et al.*, 2014). The reaction of ROS causes damage in the cellular proteins, lipids, carbohydrates, nucleotides and fats (Qwele *et al.*, 2013; Yang *et al.*, 2013; Zulkifli, 2013). ROS can also initiate lipid peroxidation and DNA damage, leading to mutagenesis and cell death (Bulut *et al.*, 2013; Durgut *et al.*, 2013; Yang *et al.*, 2013). ROS are chemically reactive molecules that contain oxygen and are important in cell signalling and homeostasis, especially when an animal experiences environmental stress (Panday & Rizvi, 2010; Falowo *et al.*, 2014). When an animal is stressed by an unusual environment, ROS concentration increases, leading to oxidative stress. Physiological stress and distress are associated mostly with higher levels of oxidative damage (Aschbacher *et al.*, 2013).

Heat-shock proteins

Stress protein synthesis increases in animals in unfavourable environmental conditions (Wang & Edens, 2008; Wang *et al.*, 2013b). In a heat-shocked cell, the proteins begin to unfold and denature, resulting in the production of heat-shock proteins (HSP). The HSPs are a subgroup of molecular chaperones, which are classified into five families (HSP100, HSP90, HSP70, HSP60 and small HSPs [sHSPs]) according to their molecular weights. During this process, HSPs may bind to heat-sensitive proteins and protect them from degradation (Al-Aqil & Zulkifli, 2009). According to Ellen *et al.* (2002), under normal growth, HSPs maintain homeostasis by regulating the folding quality control of proteins. It includes stressed and non-stressed proteins that accompany unfolded polypeptides (Kopeček *et al.*, 2001). The word 'chaperone' is normally used to highlight the functions of these proteins because they are primarily concerned with protein folding and interact with other proteins.

Chaperones have an essential role in assisting the folding, assembly and transportation of newly synthesized polypeptides and in measuring the conformational status of pre-existent proteins (Ellen *et al.*, 2002; Calloni *et al.*, 2012). They prevent the irreversible aggregation of polypeptides with other proteins that are found in the cell. Chaperones are found at various stages in protein biogenesis by regulating their structure and function under normal physiological conditions, as well as during stress, resulting in protein unfolding and misfolding (Morimoto, 2008; Shahein *et al.*, 2010; Verghese *et al.*, 2012). The Hsp70 in prokaryotes is expressed in three forms: DnaK, HscA and HscC. DnaK (major bacterial Hsp70) is one of the most abundant constitutively expressed and stress-inducible chaperones in the *Escherichia coli* cytosol. Under stressful conditions, HSPs prevent inappropriate inter- and intramolecular interactions, which may lead to protein misfolding or aggregation. However, under non-stress conditions, such as intermediate temperatures, it is not indispensable (Schröder *et al.*, 1993; Sharma & Masison, 2009; Calloni *et al.*, 2012; Aggarwal *et al.*, 2013).

Molecular chaperones such as Hsp90, Hsp70 and Hsp23 regulate steroid hormone aporeceptors and kinase activities. They also function with other protein-folding activities, which include protein disulphide

isomerases and peptidylprolyl isomerases (immunophilins). The classification depends on their molecular weight, such as Hsp100, Hsp90, Hsp70, Hsp60, as well as the family of small HSPs (Kristensen *et al.*, 2004; Calloni *et al.*, 2012). They are associated with signalling molecules and steroid receptors through the establishment of Hsp70 and Hsp90 (Ellen *et al.*, 2002).

Catecholamines, cortisol and glucocorticoids

Certain stress hormones, such as epinephrine, norepinephrine and dopamine (catecholamines), are released into the blood in small quantities (Foury *et al.* 2005; Fernstrom & Fernstrom, 2007). Catecholamines are neurotransmitters and hormones that can cause weight loss through a number of mechanisms, such as lipolysis, secretion of insulin inhibition, increased blood glucose, and thermogenesis (Utsunomiya *et al.*, 2001). They have a core structure of catechol and an amine group, which includes dopamine (DA), norepinephrine (NE) and epinephrine (EPI) (Fernstrom & Fernstrom, 2007; Goldstein *et al.*, 2009). They are found in the central nervous system (CNS), peripheral nervous systems (PNS) and adrenal glands, and also release and inactivate the organization and functioning of dopaminergic and noradrenergic systems (Muchenje *et al.* 2009a). Catecholamines are associated with an increase in the activity of tyrosine hydroxylase (TH). They are synthesised from the adrenal medullary cells, which are derived from the embryonic neural crest of the kidneys (Yanagihara *et al.*, 2005).

Tyrosine hydroxylase is regulated at times by an allosteric mechanism or enzyme induction (Candice *et al.*, 1997). The medullary cells have been found to provide a convenient model for studying the inhibition of TH in neurons such as sympathetic neurons (Blanchard *et al.*, 2001). The function of transported NE in the adrenal medullary cells is inhibited by oestrogenic pollutants (Alyea & Watson, 2009). The rate-limiting enzyme in catecholamine synthesis, which is TH, indicates a selective increase in TH mRNA (mitochondria ribosomal nuclear atom). This is normally accompanied by a corresponding response in immune reactive TH protein owing to various stressors in the environment (Blanchard *et al.*, 2001; Sobek *et al.*, 2013; Janska & Kwasniak, 2014).

Catecholamines, cytokines, energy metabolism and leukocytes, including cortisol, are useful components of the metabolic and immune function. Changes in the circulation of these components may be indicators of stress (Browning & Leite-Browning, 2013). The release of catecholamines is activated through the direct pathway where neurons terminate on target organs in response to fear. Through an indirect pathway in the adrenal medullary axis, NE and EPI are released into the bloodstream. These hormones greatly affect the metabolism of glycogen, and stimulate glycogen breakdown in the muscles and, to a lesser extent, in the liver, which responds to glucagon (Morale *et al.*, 2001; Baker *et al.*, 2013). In the muscles, glycogen levels are depleted because of the availability of EPI.

Epinephrine has been recorded as helping in the breaking down of glycogen into glucose, which is converted into energy for the muscles in the presence of oxygen. High amounts of EPI in the muscles can cause muscle tremors. This is associated with the flight response and the element loses control. In most cases, release of these hormones into the bloodstream is determined by the type of stressor, such as food deprivation, dehydration, physical exertion and fear or arousal (Voet & Voet, 1995; Lefcourt & Elsasser, 2014). When an animal has exhausted its energy levels because of rough handling before slaughter, glucose is converted to energy, resulting in lactic acid and water, which later increase the pH_u of meat (O'Neill *et al.*, 2010). The actions of EPI do not facilitate the stress response alone, because cortisol is also at play.

Blood cortisol concentrations are produced in higher levels because of the stimulation of hypothalamo-pituitary-adrenal (HPA) axis (Figure 1). An active response to stress is said to be associated with the activation of the adrenal medulla and the sympathetic nervous system (Von Holleben *et al.*, 2010). The passive response is linked to the stimulation of the pituitary-adreno-cortical system (Nwe *et al.*, 1996; Foury *et al.*, 2005; Baker *et al.*, 2013). The biochemical synthesis of catecholamines is directly modified by brain concentrations of amino acids, such as tryptophan (Trp), phenylalanine (Phe) and tyrosine (Tyr), but only if they are available in the blood. They are first hydrolysed to dihydroxyphenylalanine (DOPA) by the catalytic enzyme TH. This DOPA is immediately decarboxylated to DA by the action of aromatic L-amino acid decarboxylase (Figure 2). The neurons that use DA as a transmitter inhibit the modification of enzymes. However, neurons that use NE contain an additional enzyme (DA- β -hydroxylase), which converts DA to NE, and it is further converted to EPI by neurons that contain phenylethanolamine-N-methyltransferase (Candace *et al.*, 1977; Fernstrom & Fernstrom, 2007).

Cortisol is a primary blood constituent that is normally used to quantify stress in animals (Browning & Leite-Browning, 2013; Jama, 2014). It is a major component of stress response, in conjunction with catecholamines, which can modulate immune functions. Stressful conditions lead to elevated plasma cortisol concentrations, which may also be related to PSE meat, especially in pigs (Chai *et al.*, 2010). In calves, temperament and excitability were assessed and it was reported that cortisol and catecholamines are produced when calves experience acute stress during weaning (Burdick *et al.*, 2009; O'Neill *et al.* 2010). In human beings, cortisol levels are reported to have increased owing to related abnormal behaviour (Haller *et al.*, 2005) whereas in animals they were related to aggressive and antagonistic behaviour (Reisnet *et al.*, 2007). The glucocorticoid hormone shows an important mechanism that links chronic stress with accelerated ageing.

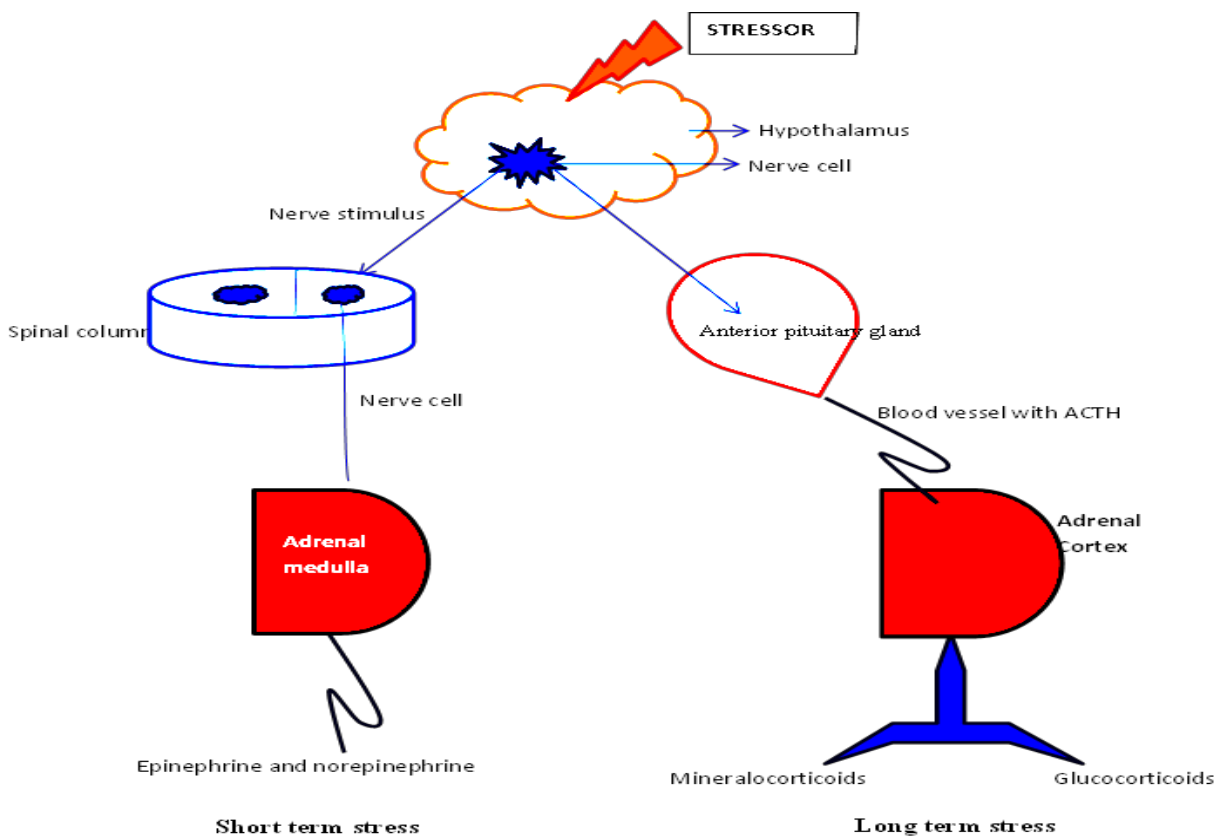


Figure 1 Schematic representation of reactions displayed by the hypothalamus, the adrenal medulla and adrenal cortex of the adrenal gland in moments of stress.

ACTH: adrenocorticotrophic hormone.

(Adapted from Burdick *et al.*, 2011).

Glucocorticoids are the effectors of the hypothalamic-pituitary-adrenal (HPA) during stress. They also modulate the immune response through gene expression, transcription, translation, post-translational processing, protein secretion and cell progenitor proliferation and differentiation (O'Connor *et al.*, 2000). During ageing, cortisol is said to be reduced when observed by the human eye, although there are increased levels when detected microscopically or electronically (Aschbacher *et al.*, 2013). A measurement of plasma cortisol is normally used to study stress reaction in animals exposed to new environments (Trevisi *et al.*, 2005; Forslund *et al.*, 2010). However, the use of cortisol as an indicator of stress requires caution. Cortisol levels may change because of several factors, such as types and severity of stressors, circadian rhythms, the blood-sampling method and non-aversive events (Trevisi *et al.*, 2005; Grandin, 2013; Seshoka *et al.*, 2013). An increase in cortisol concentration was observed in transported lambs because of the unloading, handling and bleeding procedure (Tadich *et al.*, 2009). Therefore, the interpretation of cortisol levels remains puzzling, especially in slaughter cattle.

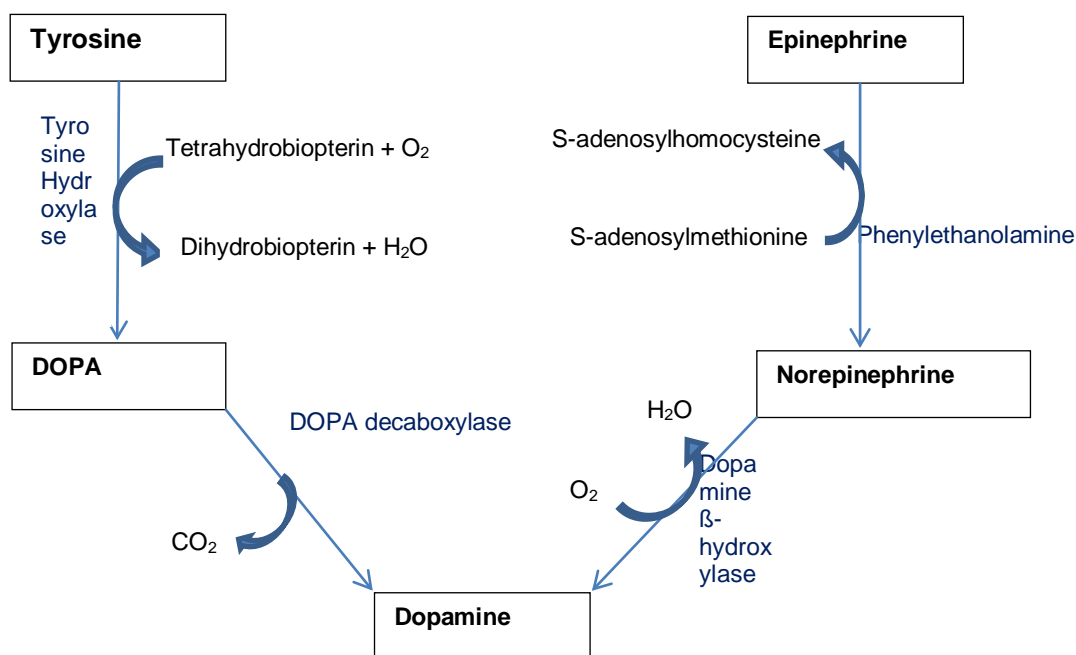


Figure 2 Biochemical synthesis of catecholamines by brain amino acids. (Adapted from Candace *et al.*, 1977).

Non-invasive assessment of methods of stress

Stress and its biological mediators are increasingly recognized as important factors that influence the rate of biological ageing in humans (Aschbacher *et al.*, 2013). However, in animals, stress is a result of aversive handling, and stunning methods used before slaughter, from which there are stress indicators that are regarded as important in determining the effects on animal welfare. Animal welfare has to do with the strong absence of negative feelings (suffering) and presence of positive feelings (pleasure). Aversive handling, such as electric prods, missed stuns, slipping in the stunning box and excessive pressure from the restraining device, results in 99% of all vocalizations in cattle, which are indications of physiological stress (Grandin, 2001; 2013). Abattoir managers increasingly monitor workers to improve animal handling and reduce the sources of stress. However, the behaviour of animals must be observed, and saliva, blood and urine samples collected to determine the hormonal-enzymatic and HSP expression (O'Connor *et al.*, 2000; Ndou *et al.*, 2011; Seshoka *et al.*, 2013) in order to examine whether the precautionary measures are effective. Various methods are used to assess the welfare of animals using non-invasive assessment (Boissy *et al.*, 2007; Geiger, 2013). These methods are said to gauge body language, interpret health and identify depression, diseases, abnormality and welfare distinctively.

These methods include physiological and biochemical approaches that are direct animal-based or indirect animal based (Duncan, 2005; Sejian *et al.*, 2011). To measure the physiological aspect of an animal, its behaviour is observed at a distance to provide information of impaired functions, such as fear and distress, hunger and thirst, injury and disease and lack of sophisticated machinery in draft animals (Bourguet *et al.*, 2011; Ndou *et al.*, 2011; Minka & Ayo, 2013). Stress because of pain, fear, discomfort, thirst and hunger that results in abnormal avoidance behaviours is caused by poor environmental conditions (Dodzi & Muchenje, 2011). Biochemical assessment for physiological response to stress entails the estimation of enzymes, hormones, glycolytic potential, proteins, lipid peroxidation, oxidative stress and tissue damage (Piccione *et al.*, 2013; Choudhary *et al.*, 2014; Falowo *et al.*, 2014).

Muchenje *et al.* (2009a) reported that in cattle raised on natural pastures, the concentration of hormones in response to stress may not be similar, because of breed differences. Fearfulness is a personal trait that drives animal behaviour and is mostly repeatable and consistent across time and situations (Njisane & Muchenje, 2013a). This is to a certain extent as a result of a new arena and a new object which can be expressions of neophobia. Neophobia is expressed by hesitation, avoidance or caution which therefore indicates the animal's internal state of risk as well as the degree of boldness (fear of novelty) (Mettler & Shivik, 2007; MacKay *et al.*, 2013). According to Mintline *et al.* (2013), calves normally exhibit play behaviour when they are excited.

As shown in Table 1, animals display different behaviours during transportation and at the abattoir depending on the type of stimulus. The assessment of animal behaviour is still a highly debated issue in

domestic animals as is the question of behavioural indicators in response to fear or pain during pre-slaughter (Boissy *et al.*, 2005; MacKay *et al.*, 2013). In wintering birds, a form of aggressive behaviour was shown because of food conflicts in hungry individuals (Lange & Leimar, 2001). This could simply mean that there are different behaviours that animals exhibit to express their feelings (anxiety, temperament, aggressiveness, excitement and boldness). However, fear is the key to the behaviours shown by animals in certain instances and during cattle handling by humans (Harris & Knowlton, 2001; Sant'Anna & Paranhos da Costa, 2013).

Table 1 Different avoidance behaviours shown by livestock before slaughter

Species	Pre-slaughter stress	Behaviour	Positive or negative	References
Birds	Hunger	Aggressive	Negative	Lange & Leimar (2001)
Calves	Touching	Play	Positive	Cloutier <i>et al.</i> (2012); Mintline <i>et al.</i> (2013)
Pigs	Transportation and at the lairages	Fear	Negative	Hemsworth <i>et al.</i> (1996); Ali <i>et al.</i> (2006); Murphy <i>et al.</i> (2014)
All species	Lairages, stunning box	Stress	Negative	Reefman <i>et al.</i> (2009); Hultgren <i>et al.</i> (2014); Njisane & Muchenje (2013a)
Cattle	Handling	Fear	Negative	Harris & Knowlton (2001); Von Keyserlingk <i>et al.</i> (2009); Hultgren <i>et al.</i> (2014); Sant'Anna & Paranhos da Costa (2013)
Cattle	Handling and equipment problems	Vocalization	Negative	Grandin (2001; 2013); Dodzi & Muchenje (2011)
Cattle	Gentle touching	Reduces fear	Positive	Voslářová <i>et al.</i> (2010); Ohl & Van der Stay (2012); Probst <i>et al.</i> (2012)
Cattle, sheep and pigs	Housing transporting	Reduces heat loss, mortality	Negative	Caulfield <i>et al.</i> (2014)
Dairy	Claw trimming	Lameness	Negative	Becker <i>et al.</i> (2014)

Discomfort experienced by animals during lairage and the movement of animals to the point of stunning before death may lead to avoidance behaviours (Grandin, 2006; Von Keyserlingk *et al.*, 2009; Njisane & Muchenje, 2013a; 2013b). The main causes associated with animal welfare problems at slaughter are categorised into five aspects (Wilkins *et al.*, 2005; Grandin, 2013);

- Poor condition of the animal
- Lack of employee training in principles of animal behaviour and methods of humane handling
- Physical distractions that impede movement of animals as they are handled
- Stressful equipment methods
- Poor maintenance of equipment (captive bolt for stunning and slippery flooring)

Wide behavioural variability has been shown by animals of the same species, same genotype and those that are reared under the same conditions (Miranda-de la Lama *et al.*, 2011). These behavioural observations have been used only in a general way without quantification such as signs of distress (jumping, bellowing, trembling, moving backwards and frequent urination). It has been reported that animals waiting for slaughter could be stressed by handling and novelty of the pre-slaughter environment (that is, the abattoir set-up), adverse weather conditions, hunger, thirst and fatigue (Muchenje *et al.*, 2009a; Bourguet *et al.*, 2011; Njisane & Muchenje, 20013a). A combination of behavioural and physiological measures has been used to assess animal welfare (Broom, 2000; Ndou *et al.*, 2011). Some studies have shown that cattle and sheep react to stressful settings (for example at the abattoir) with increased concentrations of catecholamines and creatine kinase (Vojtic, 2000; Muchenje *et al.*, 2009a). Release of these hormones and enzymes has an effect on meat quality because of rapid glycolysis and increased lactate production, resulting in elevated blood lactate (Lewis *et al.*, 2006).

Stress has been found to cause modifications to the immune system because of the physiological changes that occur (Ekiz *et al.*, 2012). These include increased heart rate, respiratory rate and temperature. Stress in pigs activates the hypothalamic pituitary-adrenal axis, and releases glucocorticoids into the bloodstream (O'Connor *et al.*, 2000; Lewis *et al.*, 2006). Cattle that are excited have increased stress responsiveness to handling, and produce more cortisol concentrations than calmer animals. This is because

cattle with excitable temperaments are less easy to handle when exposed to new surroundings (Boissy *et al.*, 2005). In general, an increase in physiological stress or physical activity in farm animals during pre-slaughter handling leads to depletion of muscle glycogen reserves before slaughter. This has a great effect on pH_u, water-holding capacity, dark cutting beef and reduced tenderness of meat (Muchenje *et al.*, 2009b; Ekiz *et al.*, 2012). However, if animals become accustomed to humans at an early stage in life, fear of humans and stress-related behaviours at the abattoir are reduced (Probst *et al.*, 2013).

Structural changes in meat

Meat quality is a term that is used by consumers, retailers, abattoir managers, farmers and the industry at large. This is because meat is the end product in beef production (Gebresenbet *et al.*, 2011; Northen, 2011). However, animals may not produce the same levels of carcass and intramuscular fat, colour, pH and tenderness because of differences in genotype, age, sex, type of production systems, pre-slaughter conditions and post-mortem changes during meat processing and storage (Muchenje *et al.*, 2008; Sentandreu & Sentandreu, 2011). The slaughter environments and processing of meat affect the quality of meat. Meat with increased pH_u results in tougher and darker meat, which is not always ideal for human consumption (Dalla Costa *et al.*, 2007; Dubost *et al.*, 2013). These attributes are also the result of bruising before and during slaughter. Therefore, it is important to understand the effects of pre-slaughter stress and avoidance behaviour of cattle and how they relate to beef quality. Meat is expected to be safe in terms of composition and appearance with more flavour (Hoffman *et al.*, 2007).

Meat makes a valuable contribution to the diet of humans as it provides concentrated proteins, iron, zinc and vitamins A and B. However, it is unfortunate that meat is highly perishable because it provides a good medium for the growth of micro-organisms. This leads to discolouration, reduced flavour, and a lower nutritional value and safety of meat (FAO, 2014b). Consumer demand for meat quality is determined by palatability, appearance, ease of preparation and tenderness (Tschirhart-Hoelscher *et al.*, 2006; Mohrhauser *et al.*, 2014). Meat quality attributes that are normally used by consumers to judge meat include colour, juiciness and tenderness. A desirable colour or appearance is expected to be uniform throughout the cut (Muchenje *et al.*, 2009b; Peña *et al.*, 2009; Mapiye *et al.*, 2010). Critical consumer quality requirements that may be altered by processing and preparing meat include fatty acid profiles, vitamins, minerals and proteins. The quantity of collagen in a muscle determines the amount of connective tissues and tenderness. In addition, intramuscular lipid content plays an important role in flavour and indirectly juiciness and tenderness (Muchenje *et al.*, 2009b; Dubost *et al.*, 2013; Modzelewska-Kapitula *et al.*, 2014).

The percentage of marbling in the meat affects its juiciness, flavour and tenderness (Hoffman *et al.*, 2007; Dubost *et al.*, 2013). Table 2 summarizes some of the structural changes that occur in meat as a result of animal-related factors (age, genotype, class and sex) during the ante- and post-mortem period. Animals that are stressed before slaughter have a rapid release of glucagon from glycogen breakdown into the blood stream. This in turn becomes broken down into lactic acid, especially in warm carcasses. Lactic acid accumulation damages the structure of the muscle, leading to loss of water and PSE meat (Grandin, 2000; Young *et al.*, 2004). One of the quality parameters of raw meat is its ability to retain moisture. The muscle stores water in the sarcolemma, which is reduced because of several factors during meat handling and processing (Huff-Lonergan & Lonergan, 2005).

The amount of collagen and the stability of cross-ridges increase as the animal advances in age, causing reduced tenderness (Petracci & Cavani, 2012). Collagen contains a large proportion of proline and hydroxyproline that is directly related to the thermal stability of the triple helix. The triple helix structure is important in the eating quality of meat. The difficulty in breaking down collagen is because of the formation of non-reducible links as a result of three or more chains (3-dimensional network) (Saha *et al.*, 2013). Short fibres affect the sarcomere length, hence the meat becomes tough. Tougher meat is DFD meat, especially from animals that were starved for too long.

During starvation, there is rapid utilization of glycogen in the muscle so that lactic acid production is reduced, leading to DFD meat instead of red firm and non-exudative (RFN) meat (Gajana *et al.*, 2013). DFM meat has a reduced shelf life because low acidity in the meat favours bacterial growth. PSE and DFD meat are both difficult to process because of low water-binding capacity and susceptibility to rigor mortis. After slaughter, glycogen reserves in the muscles are exhausted, leading to rigor mortis (stiffening of the muscles). Rigor mortis is the result of contraction in muscle fibres because of the cross-ridges that form between thick and thin filaments. Tougher meat from older animals can be remedied by cooking it for a long period at a low temperature to hydrolyse the connective tissue, though some nutrients might be affected. Tenderness is one of the most important meat quality characteristics that influence consumers' perceptions. It is considered a complex multi-factorial trait, which has been described according to the actomyosin effect of myofibrillar proteins, the background effect of connective tissue, and the bulk density or lubricating effect of fat (Hugo

et al., 2009; Naveena *et al.*, 2011; Joo *et al.*, 2013). This is because as the animal advances in age, the collagen in connective tissues becomes more complex and stronger.

Several factors influence the colour of meat including enzymes, diet, animal-related factors (age, genotype and sex), transportation and the amount of fat cover of the muscle. Colour is related to the level of the protein and myoglobin pigment in the muscle (Muchenje *et al.*, 2009b; Frylinck *et al.*, 2013). There is now considerable emphasis on modifying the fatty acid composition of animal tissues to produce 'healthier' foods. Food is termed 'healthy' if it can be digested immediately after it has been consumed. However, sometimes changes occur in the meat processing that alter the quality. During cooking, meat shrinks and some denaturing of protein in fibres occurs, which leads to hardened tissues. This then reduces the intake of protein as some of it becomes indigestible when cooked at high temperatures (Kandeepan *et al.*, 2013; Kaur *et al.*, 2014). Water-soluble compounds (amino acids, peptides and glycoproteins), lipids (polyunsaturated fatty acids of phospholipids) and Maillard reactions (heterocyclic compounds) are at play during cooking to improve flavour (Dubost *et al.*, 2013; Zuckerman *et al.*, 2013). However, because of the formation of lipid oxidation with carbonyl compounds, an abnormal flavour could be produced.

Oxidation is one of the major causes of quality deterioration in meat because of high concentrations of unsaturated lipids, heme pigments and metal catalysts, and a range of oxidizing agents in the muscle (Falowo *et al.*, 2014). It is associated with an increase in the production of oxidising agents and/or decrease in the effectiveness of antioxidant defences, such as glutathione (Lykkesfeldt & Svendsen, 2007; Zhong & Zhou, 2013). Ahhmed *et al.* (2013) showed that because of the series of processes and treatment of meat, the muscle structure and proteins undergo physico-chemical changes. Proteins and fats are hydrolysed because of the presence of endogenous enzymes, which alter the flavour of meat. Lipids and proteins are susceptible to oxidative damage because of a rapid depletion of endogenous antioxidants after slaughter.

Table 2 Structural changes that occur in meat during pre- and post-mortem treatment

Treatment	Response variable	Changes	References
Animal-related factors (age, sex, genotype, slaughter weight)	Fatty acids, pH, colour, cooking loss	↑	Yang <i>et al.</i> (2002); Dhanda <i>et al.</i> (2003); Simela <i>et al.</i> (2004); Peña <i>et al.</i> (2009)
Pre-slaughter handling (farm, transportation, truck size, stocking density, lairages)	Intensified physical activity, bruises, pH, DFD beef, PSE pork non-esterified fatty acids (NEFA),	↑	O'Neill <i>et al.</i> (2010); Dalla Costa <i>et al.</i> (2007); Von Holleben <i>et al.</i> (2009); Marenčić <i>et al.</i> (2009); Strappini <i>et al.</i> (2012); Gajana <i>et al.</i> (2013); Koknaroglu & Akunal (2013)
Post-mortem (storage, cooking method, salting and curing)	Cholesterol and saturated fat, tenderness, flavour protein content, metmyoglobin content	↓	Tateo <i>et al.</i> (2008); Muchenje <i>et al.</i> (2009c)
		↑	Ahhmed <i>et al.</i> (2013); Dubost <i>et al.</i> (2013)

DFD: dark, firm and dry; PSE: pale, soft and exudative.

Oxidative stress is explained as an imbalance between oxidant and antioxidant levels in an animal. Therefore, lipid peroxidation has been suggested as a reliable marker or mechanism to evaluate the severity of oxidative stress, which is cellular injury (Taysi *et al.*, 2006; Guo *et al.*, 2013).

Opportunities for the improvement of animal welfare

Prioritization of the welfare of animals should begin on the farm, continue during transportation and be sustained at the abattoir in order to produce healthy meat from stress-free animals. Productivity can be improved through advances in various facets of production systems from conception to consumption by adopting new technologies (Webb, 2013). Zulkifli (2013) stressed that proper selection and training of farm personnel could reduce fear of humans, lessen avoidance behaviour, enhance the health of animals and improve productivity. Improving animal welfare could mean an assessment of animal-based measures (Boissy *et al.*, 2007), which is a way forward in the perfection of animal welfare, their quality of life and good quality meat that are expected by consumers.

The use of production systems for good and hygienic farming practices provides optimal animal welfare, and increases the resistance of animals, especially pigs, to infection. In addition, mitigating the old

developments performed in the field and existing knowledge to create new methods of evaluating welfare would provide appropriate tools for good animal welfare (EFSA, 2007; Sejian *et al.*, 2011). One of the problems that requires thoughtful and serious intervention in farm animals is lameness, especially in dairy production systems. Lameness influences animal welfare, reduces productivity and affects the quality of the product after slaughter. Examining lameness in farm animals requires farmers, claw trimmers, scientists, university personnel, veterinary technicians and veterinarians to collaborate in order to adequately manage and eliminate causative agents of pain (Becker *et al.*, 2014).

Miranda-de la Lama (2013) indicated that farmers need to manage the weight and number of animals that are optimal for transportation, and work with the haulier in order to deliver live and fit animals for slaughter. To improve this situation, farmers and the industry may need to apply biotechnologies and genetic selection to assist in alleviating hunger and poverty by breeding animals and crops that adapt well to the changing climate (Mitchell, 2007; Wheeler, 2013; FAO, 2014b). It is well documented that environment and breed affect some meat quality attributes. Scholtz (2007) suggested that *Bos indicus* genes should be selected for the slaughter population to solve the problems faced by the industry, although there were questions about meat quality attributes that could be improved according to market requirements. Pimentel & König (2012) suggested that genomic selection would improve the birth weight of targeted beef breeds, beef cuts, carcass proportions, intramuscular fat and muscularity score (Table 3).

Table 3 Use of genetic selection and modification for improvement of carcass and meat quality characteristics

Parameters	References	
Carcass characteristics	Birth weight, growth performance and slaughter weight	Scholtz (2007); Smith <i>et al.</i> (2007); Mortimer <i>et al.</i> (2010); Pimentel & König (2012); Freedom Food Report (2014)
	Backfat thickness in pigs, meat yield, intramuscular fat in cattle	Utrera & Van Vleck (2004); Vote <i>et al.</i> 2009; Liu <i>et al.</i> (2013); Miar <i>et al.</i> (2014)
	Muscle - bone ratios, <i>longissimus</i> muscle, breast, leg and yield grades	Utrera & Van Vleck (2004); Pimentel & König (2012)
Meat quality characteristics	Muscle temperature, ultimate pH, colour (CIE L*, a* and b*)	Commission International de l'Eclairage (1976); Abril <i>et al.</i> (2001); Gaya <i>et al.</i> (2011); Hope <i>et al.</i> (2013); Lui <i>et al.</i> (2013); Mortimer <i>et al.</i> (2014)
	Fatty acid profiles, lean carcass growth	Karamichou <i>et al.</i> (2006); Smith <i>et al.</i> (2007); Ardiyanti <i>et al.</i> (2009); Muchenje <i>et al.</i> (2009c)
	Tenderness (Warner Braztler shear force)	Warner (1928); Bratzler (1932); Hopkins & Fogarty (1998); Muchenje <i>et al.</i> (2008); Smith <i>et al.</i> (2007); Hopkins <i>et al.</i> (2010); Bagatoli <i>et al.</i> (2013); Allais <i>et al.</i> (2014)

CIE: Commission International de l'Eclairage.

Measures that include genetic selection, breeding programmes, stress response and physiological markers of positive emotions are still being investigated, since they could improve the welfare, carcass and meat quality in slaughter animals (Boissy *et al.*, 2005; Pimentel & König, 2012; Grandin, 2013). However, the relationship between animal genetics and response of cattle to handling facilities is quite complex. This is because animals behave and respond differently to stress because of their genetic characteristics, which help them to resist and cope under heat stress (Ali *et al.*, 2006; Allais *et al.*, 2014). Stress is a non-specific phenomenon that represents the consequences of the behavioural, physiological and emotional status of an animal in response to a variety of environmental stimuli (Voslářová *et al.*, 2010). These include ambient temperature, humidity, stocking density, transport and lairage duration and sometimes management on the farm and at the abattoir (Melesse *et al.*, 2011; Chen *et al.*, 2013; Miranda-de la Lama, 2013).

Conclusion

Animal welfare and meat products for consumer satisfaction are improving worldwide because of increasing consumer demands for healthy food from healthier animals. Because of the processes that are

involved in animal production, transportation, slaughter and processing, consumers are concerned about the quality of meat. Changes in climate have led to modifications in the genetic makeup of animals and to the application of biotechnology to produce animals that provide healthy food. However, increased scrutiny of animal welfare and animal-sourced food has led to growing understanding of the issues regarding the assessment of properties of meat and meat products in relation to the way in which the animals are treated. In addition, consumers require more programmes (training on livestock production, policies, communication and transportation, market information, incentives and information on technology) to be conducted that would acquaint them with the production supply chain, since they are the prime targets for production. Therefore, there is a need to refine and adopt the proposed biotechnologies and genetic modification in animals to produce more meat in this changing climate, as well as provide for the growing population that will adapt to the changing climate.

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