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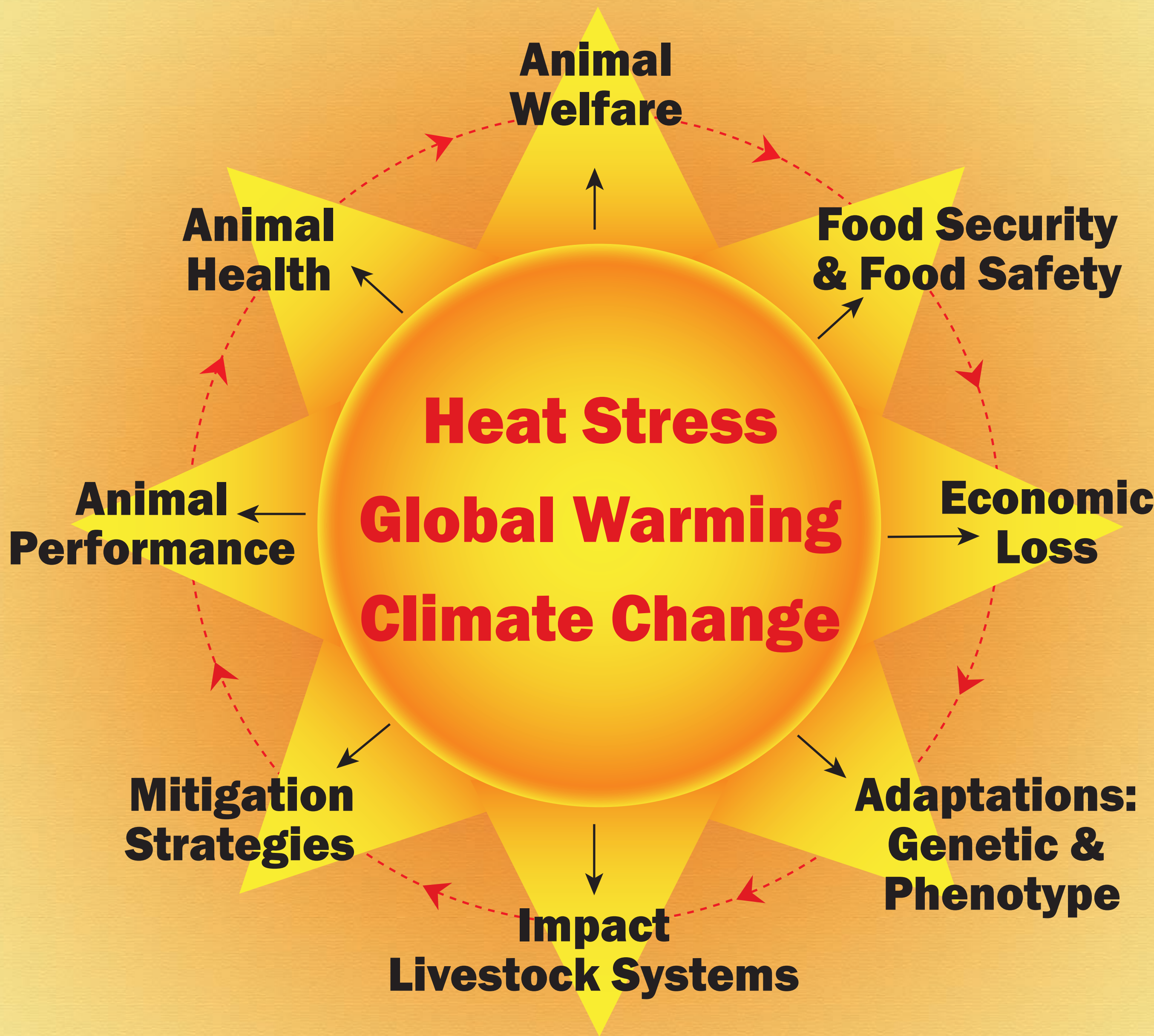

Climate Change: Impact on Livestock and How Can We Adapt

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From the Editor

Climate change: impact on livestock and how can we adapt

Umberto Bernabucci

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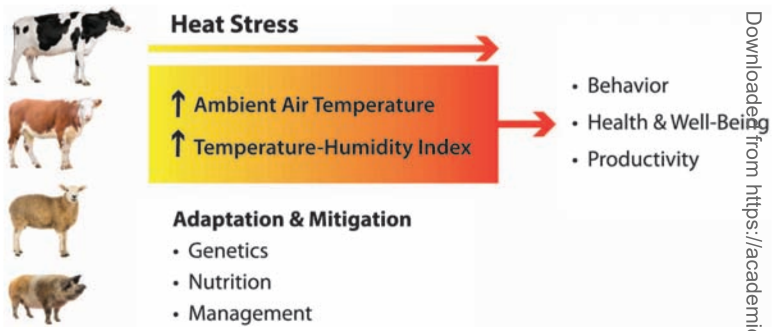

This issue of Animal Frontiers, "Climate change: impact on livestock and how can we adapt," focuses on the effects of climate change (global warming) on livestock health, well-being, production and reproduction, and on possible adaptation and mitigation strategies that can be put in place to reduce negative impacts.

Recently the intergovernmental group of experts on climate change gathered in South Korea to bring attention to the urgency of this situation: global warming is increasing and ecosystems, animal species diversity, and food security are at risk. It is now well accepted that the increasing concern with the thermal comfort of agricultural animals is justifiable not only for countries in tropical zones, but also for nations in temperate zones where high-ambient temperatures are becoming an issue. At a global level, animal production must increase in the next decades to satisfy the growing need for animal-sourced foods. We have to expect that livestock systems (based on grazing, mixed farming systems, or industrialized systems) will be more and more negatively affected by climate change, especially global warming.

The article by Pasqui and Di Giuseppe (2019) clearly shows that climate is changing. In addition to the increase in temperature, there is an increase in the frequency of extreme events such as the number of hot days and the number of heat waves. Heat waves are the combination of duration and intensity of air temperature and can strongly affect human activities as well as the health and productivity of farm animals. In recent decades, the scientific community generated much new knowledge of the fundamental mechanisms of the Earth's climate system as well as the implications and impacts of climate change. Contemporarily, an effort has been directed to identify new actions for mitigating the anthropogenic greenhouse gas emission trends, and on identifying new actions to adapt to the observed and expected changes in climate.

In the last quarter century, the livestock sector was focused on improving productivity, modifying the environment, and improving nutritional management rather than improving stress resistance. This approach dramatically increased productivity of domestic animals but also increased their sensitivity (reduced their thermal plasticity) to hot environments. The processes by which domestic animals respond to changes in their environment are critical to survival but often negatively affect productivity and profitability of livestock systems. Understanding how these processes are controlled will offer opportunities for improving thermal stress resistance. Collier et al. (2019) describe the meaning of acclimation, acclimatization, and adaptation to environmental stressors, with emphasis on heat stress. Acclimation and acclimatization are a coordinated phenotypic response to environmental stressors and the response will decay if the stressors are removed. If chronic stress persists over several generations, the acclimatization response will become genetically "fixed" and the animal will be adapted to the environment. Improving knowledge of the genetic differences between adapted animals will contribute useful information of the genes associated with acclimation. This information will be useful to help identify genes associated with improved thermotolerance.

Rust (2019) clearly shows how climate change affects both extensive and intensive livestock production systems, with emphasis on adaptation. Improving knowledge of the impact of climate change on different livestock systems and the adaptation strategies to fight climate change are of vital importance. Livestock systems, especially in developing countries, are extremely dynamic and the size and relative production output, especially in intensive animal farming practices, are increasing around the world to satisfy the growing demand for livestock products, especially in some areas characterized by adverse climatic conditions. Extensive and intensive livestock

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production systems will be affected differently by climate change and, thus, different adaptation strategies must be implemented.

Heat stress undoubtedly negatively affects animal health and welfare. Lacetera (2019) outlines how a hot environment affects farm animal health and further describes the direct and indirect effects of heat stress. The direct effects are due primarily to increased temperatures and frequency and intensity of heat waves. These environmental conditions can affect livestock health by causing metabolic disruptions, oxidative stress, and immune suppression causing infections and death. The indirect effects are those linked to alteration of the availability and the quality of feedstuffs and drinking water as well as survival and redistribution of pathogens and/or their vectors. Development and application of new methods, tools, and techniques to link climate data with disease surveillance systems should be implemented in the future for improving prevention of diseases as well as improved mitigation and adaptation responses of animals to heat stress.

Wolfenson and Roth (2019) describe how hot summer conditions disrupt several reproductive processes, resulting in a pronounced depression of conception rate in dairy cows worldwide. When body temperature reaches 39.5 °C a strong impairment of reproductive processes such as disruption of oocyte developmental competence, attenuated embryonic growth and early embryonic death due to impairment of hormone secretion, alteration of ovarian follicular growth dynamics, suboptimal development of the corpus luteum, and attenuated uterine endometrial responses may occur. Application of efficient cooling is a must and a prerequisite to minimize heat stress. However, sometimes it is not enough to lessen heat stress during summer to sustain reproductive function even when the stressor ends. It is suggested that cooling must be combined with other treatments to improve fertility. In particular, treatments for improving the timing of ovulation, enhanced removal of impaired follicles, induction of ovulation of healthy follicles, embryo transfer, and progesterone supplementation before and after artificial insemination may be needed to improve fertility of heat-stressed dairy cows.

Heat stress negatively affects milk and meat production. In addition to quantity, the quality of animal products is strongly and negatively affected by a hot environment. With regard to milk, heat stress has a more important effect on high-quality products such as the protected designation of origin cheeses from many European countries that have a world-renown reputation for excellence. Summer et al. (2019) point out the negative effects of heat stress on the composition of milk (organic and inorganic components) and describe how those changes are strongly associated with the alteration of cheesemaking properties and the merchandise value of milk. These changes result in significant, negative economic impacts for producers and consumers. Beef cattle, with their lower metabolic rate and lower body heat production, are usually considered less sensitive to heat stress than dairy cattle. However, beef cattle also compensate for increased body temperature by homeostatic mechanisms (panting, sweating, and urination) and behavioral alterations such as reduced activity, increased water intake, and reduced feed intake. These effects are responsible for generally lower growth rate and reduced fertility of both males and females.

Gaughan et al. (2019) address an important topic that is and will be a source of debate among researchers: why animals have to adapt and which strategies will be the best for adaptation? Animal adaptation is a function of several factors which are interrelated. All factors that will either enhance or reduce adaptability must be considered. It is well known that selection of animals for high levels of production has increased animal susceptibility to environmental challenges. On the other hand, using lower production cows could reduce heat stress, but reduced production efficiency may lead to increased greenhouse gas intensity. Even if a single stressor may be important, the cumulative effects of multiple stressors (in addition to heat stress) may be significant and must be considered. Adaptation strategies include production system adjustments and genetic improvement for thermotolerance. In addition to adaptation, mitigation strategies should also be addressed. These include changes in animal management systems (nutritional interventions, manipulation of the rumen eco-system, provision of shade, housing, fans, and sprinklers). Multidisciplinary approaches including animal breeding, nutrition, housing, and health are required for reducing the adverse impact of climate change on livestock.

Globally, pork is one of the most consumed animal-sourced foods. Reduced and inconsistent growth, decreased feed efficiency, decreased carcass quality (increased lipid deposition and decreased protein accretion), poor sow performance, decreased reproductive performance (male and female), increased mortality (especially in sows and market hogs), and morbidity are the main economic losses associated with heat stress in the swine industry (Mayorga et al., 2019). Evidence suggests that maternal exposure to heat stress has long-lasting effects on postnatal offspring performance. The combination of climate change forecasts, increased pork production in tropical and subtropical regions of the globe and improved genetic capacity for lean tissue accretion and fecundity, all point to increasingly negative impacts of heat stress on pork production efficiency and quality in the future. Physically modifying the environment is currently the primary abatement strategy that should be utilized to mitigate the negative effects of heat stress. Additional approaches including dietary modifications and genetic improvement may help improve mitigation and adaptation of pigs to adverse environmental conditions.

The article by Carabaño et al. (2019) explores the possibility of selecting farm animals for thermotolerance. Genetic selection is a cost-effective tool to achieve a permanent change in an animal's tolerance to heat, even though implementing selection strategies is challenging because of the complexity of the heat stress response and the antagonism between heat tolerance and productivity. To effectively select animals, there is a need to find phenotypic measures that accurately identify heat-tolerant animals and that can be used under field conditions with low cost. In addition, developing methods to efficiently combine knowledge from all "omics" technologies to produce genetic indices to perform selection of the best breeding stock is needed. Genetic improvement for heat-tolerant livestock is effective according to the production system. Systems that can provide enough resources to insure high productivity of animals will benefit more from including heat tolerance in the breeding programs of the already selected breeds for high production. In contrast, production systems with scarce resources and harsh parasite environments will benefit more from crossing local stock with highly specialized, productive breeds.

Grossi et al. (2019) debate a different topic from those addressed in the previous articles. This article focuses on the effects of livestock on the climate and discusses the main greenhouse gas emissions of the livestock sector. The livestock sector requires a significant amount of natural resources and is responsible for greenhouse gas emissions (methane and nitrous oxide). Greenhouse gases mainly come from enteric fermentation, manure storage and feed production. Implementation of mitigation strategies aimed at reducing emissions from the livestock sector is needed to limit the environmental burden from food production while ensuring a sufficient supply of food for a growing world population. Mitigation may occur directly by reducing the amount of greenhouse gases emitted or indirectly through the improvement of production efficiency. To increase the effectiveness of these strategies, the complex interactions among the components of livestock production systems must be taken into account to avoid environmental trade-offs.

Food and water security will be one of the priorities for human kind in the future. During this same time, the world will experience a change in the global climate that will cause shifts in the local climate that will affect local and global agriculture. It is now accepted that warming of the climate is unequivocal and anthropogenic warming will continue due to time scales associated with climate processes and feedback. Surface air warming in the 21st century, by best estimates, will range from 1.1 to 2.9 °C for a "low scenario" and 2.4 to 6.4 °C for a "high scenario." Decision makers, research institutions, and extension services must support livestock activities to cope at best with the loss of production efficiency, decreased quality of animal products, and enlargement of land desertification and the worsening of animal health under the expected effects of climate change in the next decades.

About the Author

Umberto Bernabucci is a professor in Environmental Physiology and Ruminant Nutrition at the Department of Agriculture and Forests Science, University of Tuscia-Viterbo, Italy. He is active, for over 20 yr, in the areas of feeding and management of heat-stressed dairy cows. He is Chair of the Master Courses in Agricultural Biotechnology and Director of the Clinical Biochemistry and Immunology Lab at the Department of Agriculture and Forests Science. His current research involves studies on the following: interactions between lipid metabolism, metabolic diseases, immune response, and oxidative status in dairy ruminants with particular attention to the peripartum period; adipokines and energy homeostasis; effects of heat stress on physiology, health, and performance of dairy cows; and nutraceutical properties of milk and cheeses.

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Feature Article

Climate change, future warming, and adaptation in Europe

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Implications

- In recent decades, the increased temperatures reported in Europe and in the Mediterranean basin represent one of the clearest footprints of climate change along with increased frequency of heat waves.
- These climate modifications put the environment and human activities under strong pressure with a resulting need for designing new adaptation and mitigation strategies.
- The climate change challenge is unprecedented for humanity and is recognized as a priority topic for future research. Changes in the way we think and behave are critical challenges at the global and regional levels.

Key words: heat waves, impacts, perception, vulnerability

Introduction

Climate change is a fundamental challenge for humanity as it deeply and pervasively affects the way we live on the planet. All human activities are affected by climate variability, which is due to natural factors (changes of natural cycles of atmospheric and oceanic mechanisms) and anthropic activities (greenhouse gas production). Climate change has an extremely heterogeneous character in terms of space, temporal variability, and distribution. This peculiarity implies the need to identify key local factors for the geographical area of interest along with knowledge of remote forces and an effective multidisciplinary approach to tackle its negatives impacts.

Climate change has been a relevant issue at the international level since the late 1980s with the creation of the Intergovernmental Panel on Climate Change by the United Nation General Assembly (Resolution 43/53, 1988). Subsequently, the Intergovernmental Panel on Climate Change First Assessment Report (IPCC, 1990) stated, "… *there is a natural greenhouse effect which already keeps the Earth warmer than it would otherwise be; emissions resulting from human activities are substantially increasing the atmospheric concentrations of the greenhouse gases carbon dioxide, methane, chlorofluorocarbons and nitrous oxide. These increases will enhance the greenhouse effect, resulting on average in an additional warming of the Earth's surface*" (IPCC, 1990). This large scale and organized scientific assessment provided the initial basis for the interpretation a deep modification of the earth's climate system. During the past three decades, more assessments of climate change have been produced by the Intergovernmental Panel on Climate Change, all of them drawn on the work of hundreds of scientists from around the world (IPCC, 2013, 2014a, 2014b).

The phase of intense global warming we experienced in recent decades began unequivocally in the 1950s and has accelerated since the 1980s (IPCC, 2014a, 2014b; Baldi et al., 2006; Zampieri et al., 2016). This increase affected both the average monthly temperature and seasonal values along with extreme climate events (IPCC, 2014a, 2014b).

Global Warming and Heat Waves

Global warming (Figure 1) produces effects that are measurable through physical indicators such as rising sea levels, increased heat content of the oceans, decreased snow and ice surface coverage (both marine and terrestrial), and increased frequency of very hot days and of very intense rains (IPCC, 2014b). Among these climate change features, extreme events are largely relevant for assessing impacts and defining coping options. For simplicity, an extreme event is defined as a climate event in which the related physical values overpass a threshold which is close to the extreme possible values for that variable (IPCC, 2012).

In this regard, a collection of 27 weather-climatic indicators were established to identify the occurrence of extreme events for monitoring purposes and for future projections of climate (Sillmann et al., 2013a, 2013b).

Projections for the 21st century by the 27 member Expert Team on Climate Change Detection and Indices indicators carried out on the basis of different climate models and different carbon dioxide emission scenarios indicate an increase in the frequency of extremely hot days and an increased number of consecutive hot days (Sillmann et al., 2013b) as shown in Figures 2 and 3.

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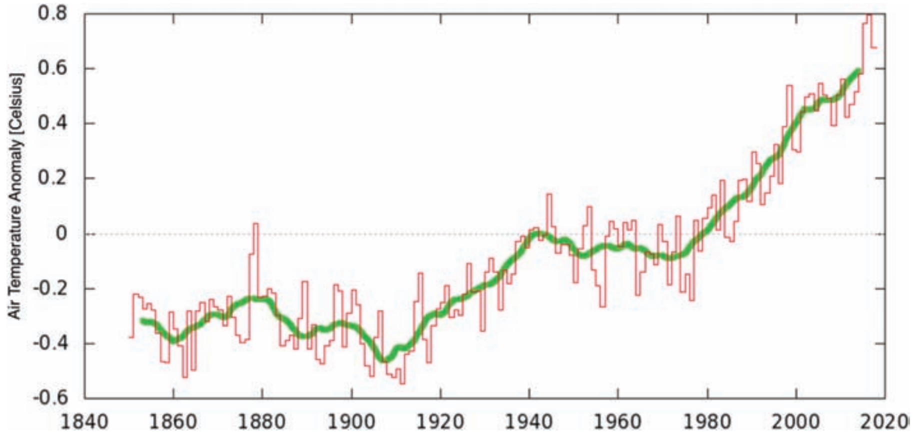

Figure 1. Annual global mean air temperature anomaly (°C) at the surface (Jan–Dec), based on the HadCRUT4 global temperature dataset (https://crudata.uea.ac.uk/cru/data/temperature/). The time series is computed with the KNMI Climate Explorer.

There are some characteristics of the climate change footprint that exhibit a more extensive nature. In Europe, among these climate change footprints, we must certainly highlight the increase in summer temperatures and a coherent increase of hot days and heat waves (Zampieri et al., 2016). There is no specific definition of a heat wave; each heat wave arises from the need to characterize the effects of the increase in temperature for long periods in a special specific sector of interest such as human health, crop production, livestock production, and the environment. Certainly, heat waves are relevant for all aspects that are intrinsically linked to factors of "suffering from heat," to which living beings in general are subjected (McMichael et al., 2006; Lacetera et al., 2013; Özkan et al., 2016). These extreme periods are referenced as high-impact weather events, along with other completely different events such as floods, wind storms, or cold waves. Heat waves could be classified according to their duration and/or their intensity which is measured by the amount that the recorded air temperature deviates from the reference climatological values. It is the combination of these features, duration and intensity, which determines effects on human activities and on the health of animals.

Based on the indications provided by the Expert Team on Climate Change Detection and Indices working group, a heat wave can be defined as the phenomenon for which there is a sequence of at least 6 days with maximum daily temperature or temperature daily minimum above the corresponding daily threshold value at the 90th percentile (Karl et al., 1999). More specifically, it is calculated as a series of daily values for the

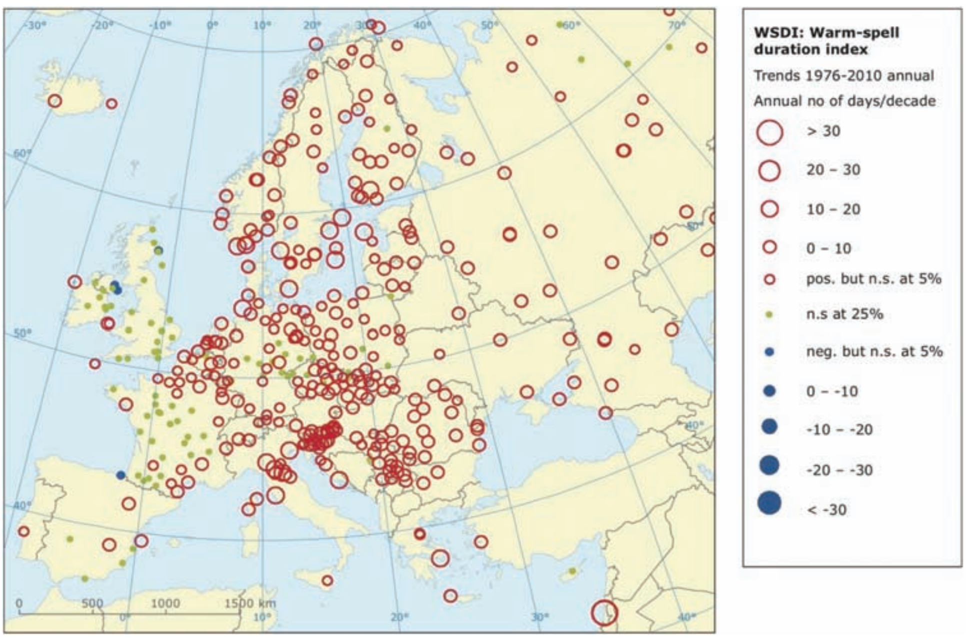

Figure 2. Warm spell duration index computed trends for 1976–2010. Circles represent the annual mean number of days for the decade. Map is from European Climate Assessment and Dataset E-OBS gridded dataset (https://www.ecad.eu).

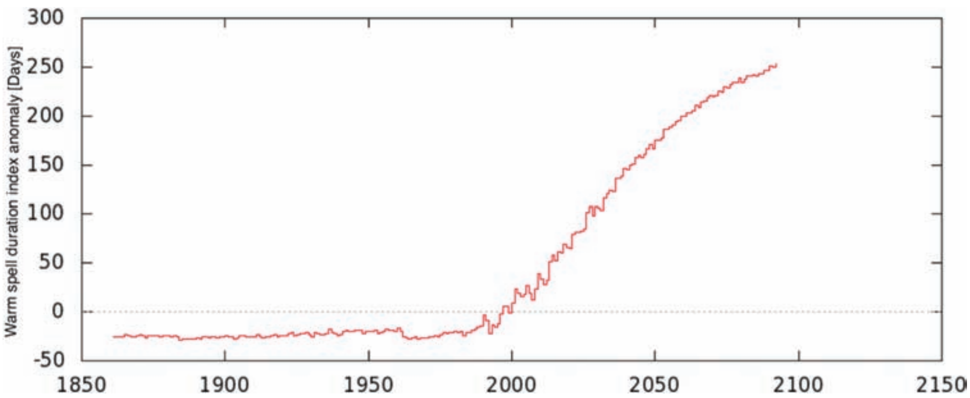

Figure 3. Warm spell duration index annual anomaly for the historical + RCP8.5 ensemble mean CMIP5 future climate scenarios (with respect to the 1981–2010 reference period). The WSDI index is averaged over the Europe geographical domain (−10°E–45°E and 35°N–65°N). Only land grid points have been taken into account. In the vertical axis, the annual mean anomalous number of WSDI-ETCCDI days is shown. In the horizontal axis, time span is shown. Data and computation from the KNMI Climate Explorer.

analysis period, in such a way as to have a specific threshold value for each observation day and thereafter the threshold is exceeded day by day. Thus, air temperature values during the heat wave are considerably higher than the reference climate values for that period and for that geographical area.

To characterize heat waves, the Expert Team on Climate Change Detection and Indices group defined the Warm Spell Duration Indicator index as the number of days that belong in a heat wave. Starting from weather station data, using model reanalysis and modeling future climate scenarios, it is possible to reconstruct the trends of daily air temperature anomalies and to identify hot days and heat waves.

What do we know about heat waves? In Europe, scientific studies and sector reports indicate a clear trend of an increasing number of hot days together with an increase in warm periods and heat waves (Baldi et al., 2006; Zampieri et al., 2016). The Mediterranean area is, therefore, a climate change hot spot (Giorgi, 2006), since it stands out for being one of the most critical areas for heat waves and related issues (Baldi et al., 2006; Giorgi and Lionello, 2008, Efthymiadis et al., 2011; Ulbrich et al., 2012). This specific climate signal became more evident in the second half of the 20th century. At the same time, a number of studies on future climate projections indicate how the footprint of this extreme warming feature will persist in the future. It is indeed very probable that the frequency of hot days and heat waves will increase significantly in the future. Thus, intensification is likely (Figures 1–3).

It should also be emphasized that the opposite weather conditions, characterized by the number of cold days and the number of cold waves, exhibited a significant decrease in the last 30 yr and the same trend is expected to persist in the future in Europe and in the Mediterranean basin.

Climate Change Impacts and Adaptation

In the last decades, an effort has been made by the scientific community to enhance our scientific knowledge of the fundamental mechanisms of the Earth's climate system as well as the implications and impacts of climate change. A portion of this effort has been directed to identify the new actions for mitigating anthropogenic greenhouse gas emission trends. Other efforts have focused on identifying new actions to adapt to the observed and expected changes in climate (IPCC, 2013, 2014a, 2014b).

Thus, defining and designing salient actions to tackle the negative effects of climate change must be planned at the local scale to guarantee their effectiveness. To be legitimate, these actions must be developed in accordance with surrounding landscape structures and socioeconomic and environmental regional characteristics and, finally, in accordance with national and international policies.

Climate change modifies the specific thermo-physical features and frequency of occurrence of climatic events. Therefore, modification of air temperatures, precipitation amounts, air humidity levels, ventilation intensities, and occurrence of extreme events such as floods, drought, cold waves, and heat waves due to climate change produces impacts on the environment and on agricultural and livestock production systems. For these reasons, agriculture is one of the most vulnerable production sectors to the forces of climate variability and climate change.

Direct impacts of climate change on livestock can be identified. These include changes in eating behavior and changes in animal physiology. Indirect impacts of climate change on livestock are also apparent and include pathogen ecology, water resource quality, and increased mortality of individuals. Climate change also alters livestock agronomic practices and management strategies. The direct and indirect impacts of climate change are modulated by different factors such as geographical location, specific animal characteristics, the intensity of extreme events, and the level of exposure. Specific effects on animals include altered well-being, health, and conformation, which in turn have a direct effect on the quality and quantity of livestock production (Özkan et al., 2016).

Changes in the quality of livestock production force modifications on food safety, food availability, greenhouse gas emissions, and farm income variability may also have social impacts. In fact, this is the schematized and simplified process that leads to a potential change in the livestock sector from pure climatic variation. This complex network of interagent factors can be seen as an arena in which there is strong competition and potential conflict between the key factors (Köchy et al., 2017).

Climate change can modify the conditions in which farmers typically operate by introducing new levels of uncertainty, many of which were previously unknown. These complex and demanding conditions call for new motivations to adapt strategically and cope with climate change. These efforts are relevant to the complex field of livestock production, in particular, in southern European areas and in the Mediterranean (Segnalini et al., 2011), where the impact of climate change seems to be more evident and substantially negative (Dono et al., 2016). The increase in summer temperatures and the increase in number and intensity of heat waves together with a persistent reduction in water resources negatively affect dairy production. Indeed, recent studies have shown that heat waves lead to increased mortality rates in dairy cattle (Vitali et al., 2009) and a decrease in the quality and quantity of milk produced (Bertocchi et al., 2014). Therefore, climate change will have a significant economic impact on the income of the agricultural enterprise (Dono et al., 2013).

Management of livestock during heat waves is critical for livestock producers and will have an impact on the income of livestock producers. The negative effects of heat stress on livestock can be summarized as follows: 1) an increase in animal mortality rates, especially due to impaired immune responses and the spread of infectious diseases, 2) reduced fertility due to altered hormonal patterns, 3) reduced feed intake and growth rates, and 4) reduced amounts of milk, especially in high-producing dairy cows.

Furthermore, climate and environmental changes associated with high temperatures, high levels of carbon dioxide, and modification of rainfall frequency will likely affect crop production, which is fundamental for the feed and forage supply for livestock. The direct effects of climate warming and reduced rainfall are reductions in feed and forage yields, alteration of nutritional value (e.g., increased lignification), and variation of the floristic composition of the biomass. Indirect effects of climate change include diffusion of parasites and pathogens as well as increased invasiveness of some plant species. The loss of biodiversity and deteriorated soil functions due to extreme climate events must be considered within the big picture of the challenges of climate change.

Perceptions of Climate Change

In recent decades, robust scientific knowledge has been produced that provides important information that can be used to make science-based decisions. However, additional decision-support tools and an understanding of the cognitive processes associated with perceptions of climate change are needed to use this information to transform society to be resilient to climate change.

The conceptual reference framework of this cognitive process of the perception to climate adaptation (Figure 4) can be divided into several, related phases (Nguyen et al., 2016a, 2016b) as follows:

1) The first phase is when the farmer learns about local, environmental aspects through direct observations.
2) The second phase is completed when the farmer understands, through direct experience, the economic, professional, social, and cultural backgrounds of the area in which he/she operates.
3) The third phase consists of practice in a specific socioeconomic, social, cultural, and institutional setting of conditions. This stage is also enriched by social, scientific, and technological knowledge that the farmer could borrow from personal and institutional relationships.
4) The final phase is reached when there is effective transformation of decision-making processes toward a state of greater

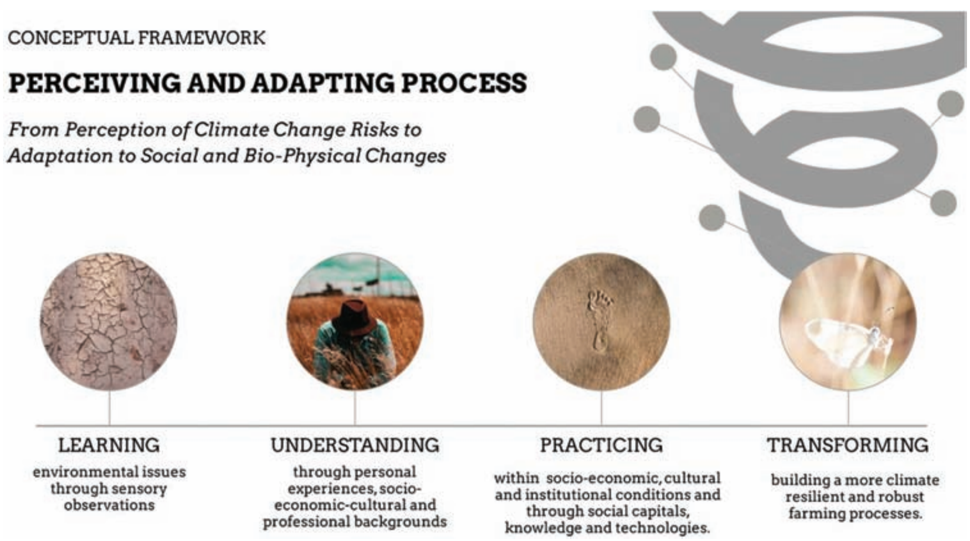

Figure 4. The cognitive process: a conceptual framework of perceiving and adapting process (adapted from Nguyen et al., 2016a).

resilience and robustness with respect to climate change.

The first two phases are driven by the farmer's personal adaptation, which is modulated by the perception of information related to risks associated with climate change. The last two phases are represented by the farmers' ability to adapt and change, which comes from biophysiological and social processes. For these reasons, the process of adaptation to climate change must be built on both dimensions of learning for adapting ("perceiving to learn and to adapt" and "learning to perceive and to adapt") in order to sustain adaptive response cycles to climate change (Nguyen et al., 2016b).

Conclusions

The challenge of climate change is unprecedented for humanity and requires a significant change in our way of thinking and acting (IPCC, 2014b). We now know, with a heterogeneous, but reasonable level of reliability, how future climate change scenarios will affect agro-ecosystems, landscapes, coastlines, agricultural yields, and local and global economies. However, how these changes will affect society, in general, are still not known.

To develop an effective climate change adaptation strategy, scientists, citizens, farmers, livestock producers, and policy makers will need to adapt a new process of thinking and learning, which must be based on current scientific information. Adaptation to climate change must be implemented as a continuous transformation, which implies continuous change at different levels of society. Institutions also play a substantial role within this transformation process. Stakeholders must be aware of the potential negative impacts and threats associated with climate change and they must be willing to engage in debate to enhance their learning and to integrate scientific and traditional knowledge to develop and implement innovative adaptation strategies. In addition, there is need for additional public–private partnerships to deal with complex issues such as those related to human health and water governance to support nonlitigious mediation of environmental conflicts.

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Feature Article

Heat stress: physiology of acclimation and adaptation

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Implications

- Climate is the biggest single factor affecting animal production.
- Acclimatization is a coordinated phenotypic response to environmental stressors and the response will decay if the stressors are removed.
- Acclimatization occurs in two phases; short term (acute stress response) and long term (chronic stress response).
- The acute phase acclimatization response is under homeostatic regulation and the chronic phase response is under homeorhetic regulation.
- If chronic stress persists over several generations, the acclimatization response will become genetically "fixed" and the animal will be adapted to the environment.

Key words: acclimation, acclimatization, adaptation, stress

Introduction

Climate is the most important ecological factor determining the growth, development, and productivity of domestic animals (Adams et al., 1998). Climate changes impact the economic viability of livestock production systems worldwide (Klinedinst et al., 1993) through a variety of routes. These include changes in food availability and quality, changes in pest and pathogen populations, alteration in immunity and both direct and indirect impacts on animal performance, such as growth, reproduction, and lactation. Lack of prior conditioning (acclimatization) to sudden change in weather often results in catastrophic losses in the domestic livestock industry (Thornton et al., 2009)

Despite uncertainties in climate variability, the Intergovernmental Panel on Climate Change (**IPCC**) Fifth Assessment Report identified the "likely range" of increase in global average surface temperature between 0.3 °C and 4.8 °C by the year 2100 (IPCC, 2014). The risk potential associated with livestock production systems due to global warming can be characterized by levels of vulnerability, as influenced by animal performance and environmental parameters (Hahn, 1995). As production levels (e.g., rate of gain, milk production per day, eggs per day) increase, the sensitivity and tolerance to stress increases and, when coupled with an adverse environment, the animal is at greater risk.

Nationally, heat stress results in total economic losses ranging between $1.9 and $2.7 billion per year (St-Pierre et al., 2003). Although projected increases in ambient temperatures will result in additional financial losses, the extra metabolic heat resulting from the projected increase in animal productivity will have far greater impact, which has been estimated at between two and four times as much as global warming (St-Pierre et al., 2003; St.-Pierre, 2013).

Our understanding of the mechanisms by which environmental stress reduces productivity of domestic animals has greatly improved over the last century (Collier et al., 2017). However, it has been difficult to genetically alter production animals to improve their tolerance to thermal stressors. For example, decades of research using genetically defined populations demonstrated that using conventional crossbreeding approaches to improve resistance to thermal stress in the dairy industry always resulted in lower milk yields in the F1 generation, the same holds true for live weight gain in meat animals (Branton et al., 1974; Frisch and Vercoe, 1977).

Therefore, improving productivity in animals exposed to adverse environmental conditions during the last quarter century focused on modifying the environment and improving nutritional management while applying selection pressure on improving yields rather than improving stress resistance. This approach dramatically increased productivity of domestic animals but also increased their sensitivity (reduced their thermal plasticity) to high temperatures in general because of their greater internal heat load.

The purpose of this review is to define processes by which domestic animals respond to changes in their environment. These processes are critical to survival but often negatively impact productivity and profitability of livestock operations. However, understanding how these processes are controlled offer opportunities for improving thermal stress resistance.

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Thermal Regulation

The thermal strategy of mammals and birds is to maintain a body temperature above the surrounding ambient temperature which allows them to dissipate heat through three mechanisms requiring a thermal gradient (conduction, convection, and radiation); collectively referred to as sensible routes of heat loss. When the thermal environment meets or exceeds the animal's body temperature these routes of heat exchange are lost, and the final/only remaining route of heat loss is through evaporative routes (sweating and panting) which require a vapor pressure gradient and dictate that relative humidity is a major factor controlling rate of evaporative heat loss. Routes of energy exchange (sensible heat and evaporative heat) are fixed by the laws of physics. However, variability among animals in body size, fat deposition, hair coat, functional activity, level of production, and number of sweat glands, as well as the presence or absence of anatomical respiratory countercurrent heat exchange capability, has led to specialization of heat exchange among domestic animals. For example, some use conductive energy exchange (swine) or respiratory exchange (ruminants, poultry), whereas horses have extremely high sweating capability (Collier and Gebremedhin, 2015).

Animals are most productive inside a range of temperatures referred to as the thermal neutral zone. When animals are exposed to conditions outside of the thermal neutral zone (cold or heat stress) they must expend energy to maintain euthermia. The temperatures at which this occurs is referred to as the upper and lower critical temperatures. The upper critical temperature is always below body temperature because of the requirement for a thermal gradient to dissipate heat by sensible routes of heat loss (conduction, convection, and radiation). As shown in Table 1, the upper and lower critical temperature of dairy cattle changes with body size, age, and level of production.

It is clear from Table 1 that although the set point remains the same throughout life and the upper critical temperature drops slightly with age and production, the big change is the drop in the lower critical temperature with increase in body size, insulation, and heat associated with metabolism of production. These factors decrease the lower critical temperature making animals more resistant to cold and less tolerant to heat.

Thermoregulation is a neural process that connects information from the external and internal thermal environment to an appropriate efferent response (e.g., vasoconstriction, raising and lowering hairs or feathers, panting), which permits the animal to maintain a stable internal environment relative to a variable external environment (Nakamura and Morrison, 2008). These efferent autonomic pathways also provide the connection between the external environment and cellular metabolism by directly regulating cellular metabolism and endocrine system activity (Collier and Gebremedhin, 2015; Figure 1).

Table 1. Effect of age and physiological state on critical temperatures of dairy cattle

	Critical temperatures		
Physiological status	Lower (°C)	Upper (°C)	Set point (°C)
Calf (4 liters milk daily)	13	26	38.5
Calf (50–200 kg, growing)	−5	26	38.5
Cow (dry and pregnant)	−14	25	38.5
Cow (peak lactation)	−25	25	38.5

Adapted from Collier et al. (1982).

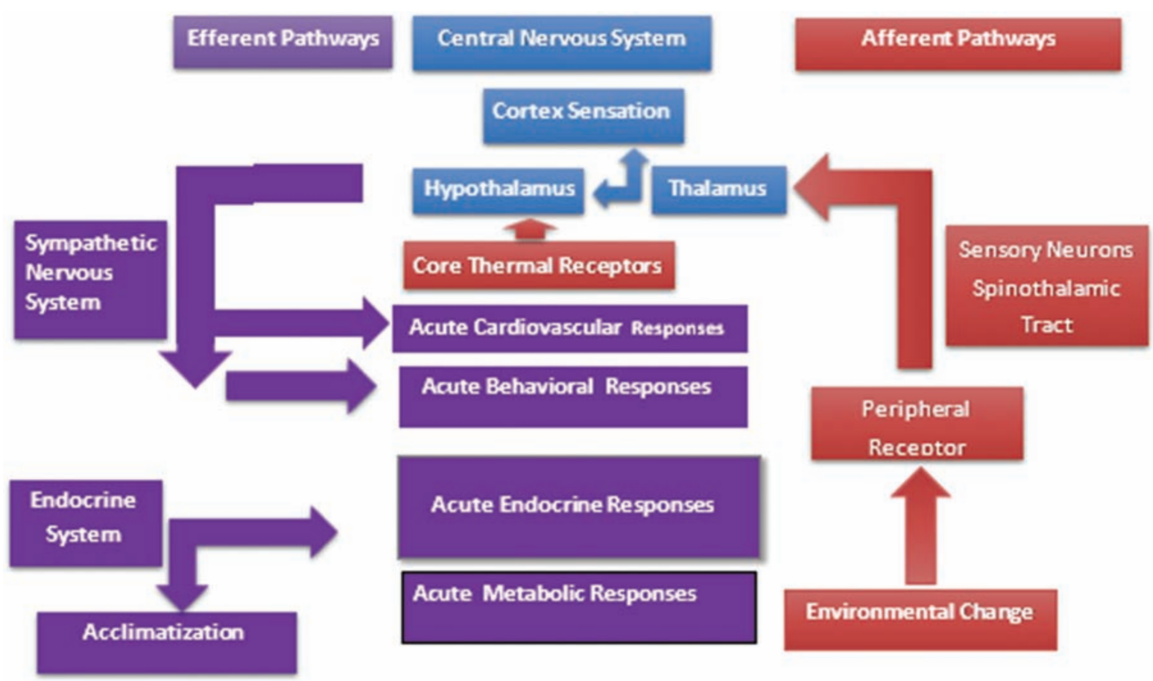

Figure 1. Schematic of neural integration of environmental conditions with animal metabolism. Adapted from Collier and Gebremedhin (2015).

Thermal Stress

Stress is defined as an external event or condition which produces a "strain" in a biological system. When the stress is environmental, the strain is measured as a change in body temperature, metabolic rate, productivity, heat conservation, and/or dissipation mechanisms. Thermal stress is triggered when environmental conditions exceed the upper or lower critical temperature of domestic animals requiring an increase in basal metabolism to deal with the stress.

Animals mount a response to a stress that involves behavioral, metabolic, and physiological changes at multiple levels of vertebrate organization from subcellular to the whole animal (Collier and Gebremedhin, 2015). The systemic response to environmental stress is driven by two systems—1) the central nervous system and 2) peripheral nervous system and endocrine components (Figure 1) (Charmandari et al., 2005). The central component involves nuclei in the hypothalamus and brainstem which release corticotrophin-releasing hormone and arginine vasopressin. The peripheral components of the stress system include the pituitary–adrenal axis, the efferent sympathetic adrenomedullary system and components of the parasympathetic system (Habib et al., 2001). However, relative to environmental stressors and acclimatization, the initial phases of the response involve receptor systems at the periphery and central receptors in the hypothalamus. Peripheral receptors include skin thermoreceptors and photoreceptors in the retina which drive autonomic and endocrine responses to the changing environment.

The stress response is divided into two phases, acute and chronic (Collier and Gebremedhin, 2015). These two stages correspond to the two stages of acclimatization to a stress. Acute stress responses last from a few minutes to a few days (Horowitz, 2002). Activation of the acute response to stress is initiated by thermal receptors located in the skin and hypothalamus which respond to changes in the environment (Collier and Gebremedhin, 2015; Figure 1). The afferent pathways for the stress transmit this information to the central nervous system including the thalamus and hypothalamus where setpoints are controlled and to the cortex for perception (Figure 1). These centers then activate various efferent pathways to induce a response to the environment, Figure 1. The acute response is driven by the autonomic nervous system promoting release of catecholamines and glucocorticoids which alter metabolism and activate transcription factors involved in the acute response. The severity of the acute stress response is affected by several factors including level of production, disease, age, body condition, and hair coat characteristics. The effect of acute heat stress on dairy cow feed intake is shown in Figure 2, which demonstrates a decrease in feed intake as the thermal environment increased from a temperature humidity index (**THI**) of 57–72.

However, if you examine the relationship between production level and thermal stress you see a different pattern. As shown in Figure 3, the higher the milk yield at the onset of acute thermal stress the greater the decrease in feed intake in lactating dairy cows. At low levels of milk yield (e.g., below 25 kg of milk per day), there is little impact of heat stress on

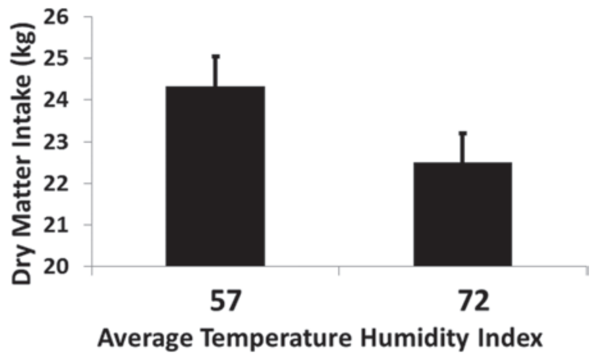

Figure 2. Effect of thermoneutral (average THI = 57) or heat stress (average THI = 72) conditions on feed intake in lactating dairy cows under controlled environmental conditions ($N = 95$, feed intake decreased 11.5%, $P < 0.001$). Data summarized from Wheelock et al. (2010); Zimbelman et al. (2010); Hall et al. (2016, 2018).

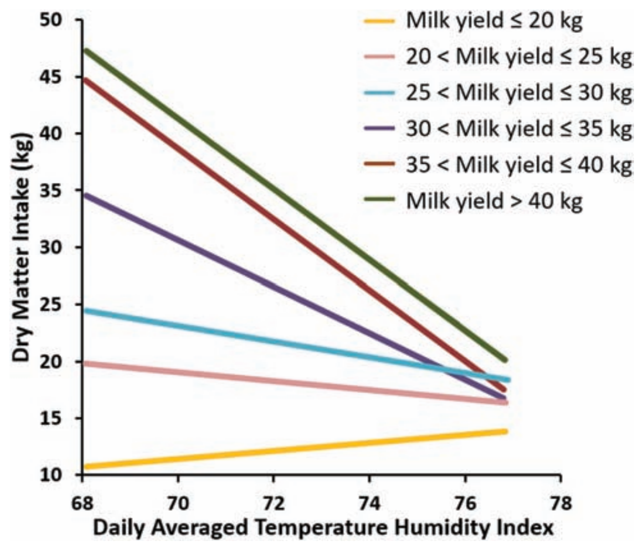

Figure 3. Effect of level of milk production on feed intake response to acute (3 days) heat stress. Data summarized from Wheelock et al. (2010); Zimbelman et al. (2010); Hall et al. (2016, 2018).

feed intake. Furthermore, the strength of the negative correlation between thermal environment and feed intake increases as daily milk yield increases as shown in Figure 3. The accelerated decline in intake of high producing animals is dictated by the need to rapidly decrease heat production to balance thermal load. This clearly demonstrates that high producing dairy cows are most susceptible to acute thermal loads.

Water intake requirements are increased in thermal stress to accommodate increased evaporative heat loss requirements. This pattern is shown in Figure 4 which depicts a 21% increase in water intake in lactating dairy cows as the thermal environment increased from a THI of 57 (thermoneutral) to a THI of 72 (heat stress).

However, if we also examine the level of milk yield at the onset of acute heat stress we see a different pattern. As shown in Figure 5, at high levels of milk yield (>30 kg milk per day) water intake decreases to acute thermal load as water requirements for milk synthesis are decreased to decrease heat production of lactation.

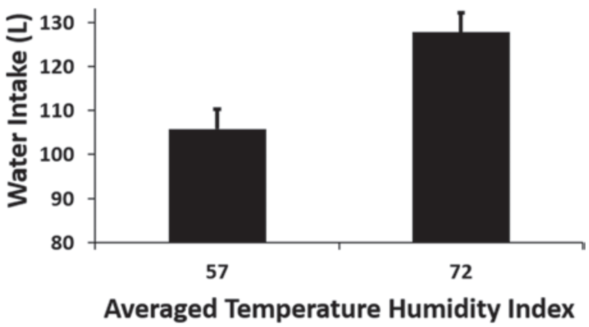

Figure 4. Effect of chronic (10 days) thermoneutral (THI = 57) or heat stress (THI = 72) conditions on water intake in lactating dairy cows under controlled environmental conditions,(N = 77, 20.8% increase, P < 0.001). Data summarized from Wheelock et al. (2010); Zimbelman et al. (2010); Hall et al. (2016, 2018).

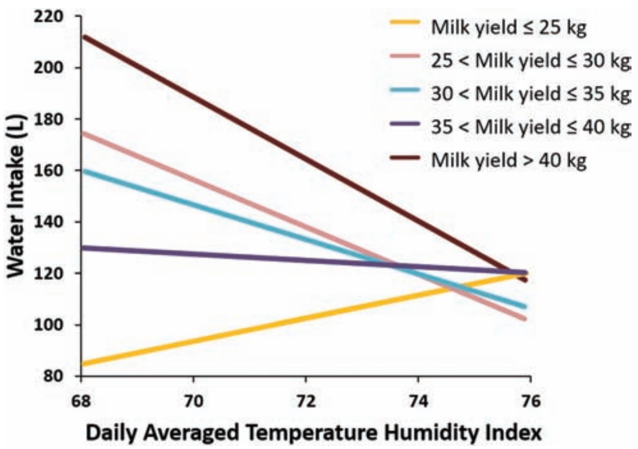

Figure 5. Effect of level of milk production on water intake response to acute heat stress conditions. Data summarized from Wheelock et al. (2010); Zimbelman et al. (2010); Hall et al. (2016, 2018).

At lower levels of milk yield the water intake does indeed increase in order to meet increased water requirements for heat loss. Thus, acute heat stress drives down milk yield by multiple mechanisms which include rapid decreases in feed and water intake in conjunction with reduced milk synthesis. The local factors regulating reduced milk synthesis have not yet been elucidated.

Acclimation, Acclimatization, and Adaptation

Animals have developed coping mechanisms to minimize the impact of these environmental stressors on their biological systems. These responses are termed acclimation, acclimatization, and adaptation. Acclimation is defined as the coordinated phenotypic response developed by the animal to a specific stressor in the environment (Fregley, 1996) while acclimatization refers to a coordinated response to several simultaneous stressors (e.g., temperature, humidity, and photoperiod; Bligh, 1976). Adaptation involves genetic changes as adverse environments persist over several generations of a species. Generally, there is hardly ever an example under normal environmental conditions where only one variable is changing. Therefore, typically an animal is undergoing acclimatization to a changing environment. Acclimation and acclimatization are induced by the environment and are considered phenotypic and not genotypic change and the responses decay if the stress is removed. Acclimation and acclimatization act to improve animal fitness to the environment. In many cases, the response is induced by sudden environmental change, such as heat or cold stress. In other examples, the acclimation response is driven by slower seasonal changes in photoperiod or other environmental cues such as the lunar cycle which permit the animal to "anticipate" the coming change in the environment leading to seasonal acclimation adjustments in insulation (coat thickness, fat deposition), feed intake, or reproductive activity in advance of the actual environmental change. However, in every case, the process is driven by the endocrine system and is "homeorhetic"; meaning metabolism is coordinated to support a specific physiologic state (Bauman and Currie, 1980). In this case, the specific physiologic state is the "acclimatized animal." If the environmental stressors are present for prolonged periods of time (e.g., years) these metabolic and physiologic adjustments can become "fixed genetically" and the animal is considered "adapted" to the environment.

Acclimation and acclimatization are therefore not processes which involve evolutionary adaptations or natural selection, which are defined as changes allowing for preferential selection of an animal's phenotype and are based on a genetic component passed to the next generation. The altered phenotype of acclimatized animals will return to the prior state if environmental stressors are removed, which is not true for animals which are genetically adapted to their environment (Collier et al., 2006). Acclimatization is a process that takes several days to weeks to occur, and close examination of this process reveals that it occurs via homeorhetic and not homeostatic mechanisms. As described by Bligh (1976), there are three functional differences between acclimatization responses and homeostatic or "reflex responses." First, the acclimatization response takes much longer to occur (days or weeks vs. seconds or minutes). Second, the acclimatization responses generally have a hormonal link in the pathway from the central nervous system to the effector cell. Third, the acclimatization effect usually alters the ability of an effector cell or organ to respond to environmental change. These acclimatization responses are characteristic of homeorhetic mechanisms as described by Bauman and Currie (1980) and the net effect is to coordinate metabolism to achieve a new physiological state. Thus, the seasonally acclimatized animal is different metabolically in winter than in summer. Bauman and Currie (1980) incorporated these characteristics of acclimatization into the concept of homeorhesis, which is defined as "orchestrated changes for priorities of a physiological state" (Bauman and Currie, 1980). The concept originated from considering how physiological processes are regulated during pregnancy and lactation (Bauman and Currie, 1980), but application of the general concept has been extended to include different physiological states, nutritional and environmental situations, and even pathological conditions. Key features of homeorhetic controls are its chronic nature, hours and days vs. seconds and minutes required for most examples of homeostatic regulation; its simultaneous influence on multiple tissues and systems that results in an overall coordinated response, which is mediated through altered responses to homeostatic signals (Bauman and Elliot, 1983).

Acclimatization is generally considered to occur in two stages; acute or short term and chronic or long term (Horowitz, 2002). The acute phase involves the heat shock response at the cellular level (Carper et al., 1987) and homeostatic endocrine, physiological, and metabolic responses at the systemic level while the chronic or long-term phase results in acclimatization to the stressors sometimes called "conditioning" and involves reprogramming of gene expression and metabolism (Horowitz, 2002; Collier et al., 2006). In domestic animals, there is generally a loss in production as animals enter the acute phase and some or even all this productivity is restored as animals undergo acclimatization to the stressors.

The chronic response or stage 2 of acclimatization to stress is driven by continued exposure of the animal to the stressor. It is mediated by the endocrine system and is associated with altered receptor populations which change tissue sensitivity to homeostatic signals resulting in a new physiologic state (Bligh, 1976; Bauman and Currie, 1980). Thus, acute heat stress is a

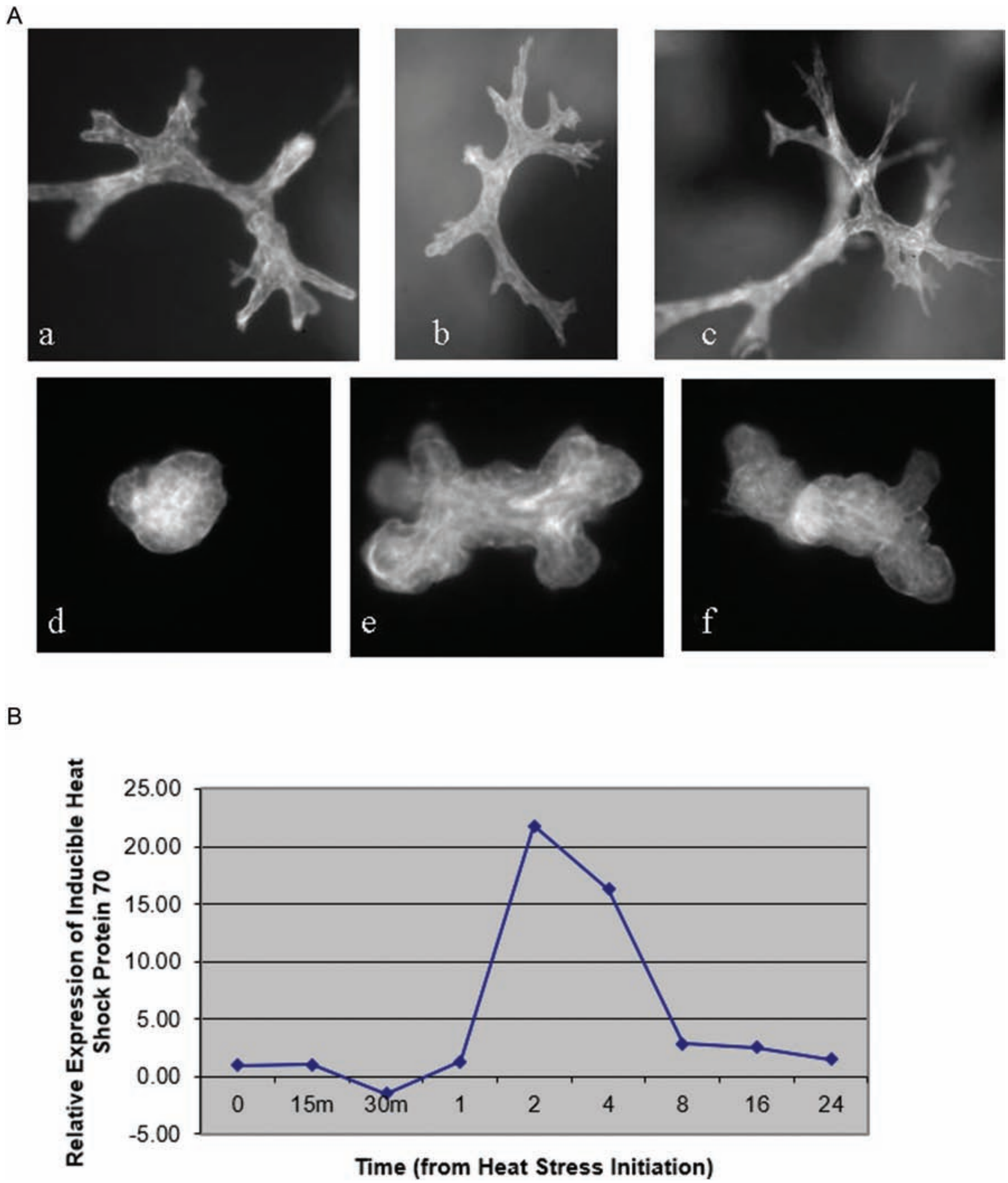

Figure 6. (A) Phalloidin stained whole mounts of bovine mammary collagen gel cultures on day 7 of culture after 24 h at either 37 °C (top) or 42 °C (bottom), (B) Relative expression of inducible HSP-70 gene RNA in response to acute thermal stress. From Collier et al. (2006).

homeostatic response driven by the autonomic nervous system and chronic stress responses, acclimatization and seasonal changes are driven by the endocrine system and homeorhetic mechanisms.

Thermal Tolerance

The degree to which animals can acclimatize to thermal environmental conditions is referred to as thermal plasticity. The thermal plasticity is affected by age, body size, disease, degree of insulation, and production level. High producing animals have reduced plasticity to environmental heat stress but increased plasticity to cold stress. The upper limit of the ability to adjust to thermal loads is referred to as thermal tolerance. The same factors which influence thermal plasticity also influence thermal tolerance when considering whole animals. At the cellular level, thermal tolerance is identified by the ability of an individual cell to maintain the production of heat shock proteins which protect against high temperature. As shown in Figure 6A, top row, when bovine mammary epithelial cells were cultured in a collagen matrix for 7 days at thermoneutral temperature (37 °C) they grew into ductal trees. When a subgroup was then subjected to heat shock (42 °C) and samples taken at regular intervals for analysis of inducible heat shock protein 70 (**HSP-70**) it was clear that the synthesis of inducible HSP 70 is increased in thermal stress for approximately 4 h but then rapidly declines (Figure 6B). This loss in ability to synthesize HSP 70 was associated with the complete collapse of the cytoskeleton at 24 h (Figure 6A, bottom row). Thus, thermotolerance of bovine mammary epithelial cells at 42 °C only lasted 4 h. The results of heat shock on bovine mammary epithelial cells in culture have previously been demonstrated in bovine embryos by Hansen and coworkers (Edwards and Hansen, 1997) who have demonstrated why bovine embryos are very susceptible to thermal shock.

The best available data on thermal tolerance of dairy cattle was published by Vitali et al. (2009) who examined the mortality records of 320,120 Italian Holstein cows over a 6-year period. They reported that seasonal patterns in mortality were identified in all 6 years. Furthermore, they demonstrated a clear relationship between THI and death rate for both maximum and minimum daily THI as shown in Figure 7.

These investigators reported that a daily afternoon maximum THI of 87 and a minimum morning THI of 77 should be considered the upper and lower daily THI values for maximum risk of death of dairy cows to heat stress (Vitali et al. 2009). It is quite possible that as we increase average milk yield per cow these critical temperature thresholds will decrease.

As pointed out by several investigators, the separate evolution of *Bos taurus*, *Bos indicus*, and Sanga cattle has resulted in *Bos indicus* and Sanga cattle developing genotypes that confer improved thermal tolerance compared with *Bos taurus* cattle in both beef and dairy populations (Kadzere et al., 2002; Hansen, 2004). Detection of large genotype × environment interactions in dairy cattle for milk yield (Ravagnolo et al., 2000; Bohmanova et al., 2008) in just the Holstein cattle population, indicates that

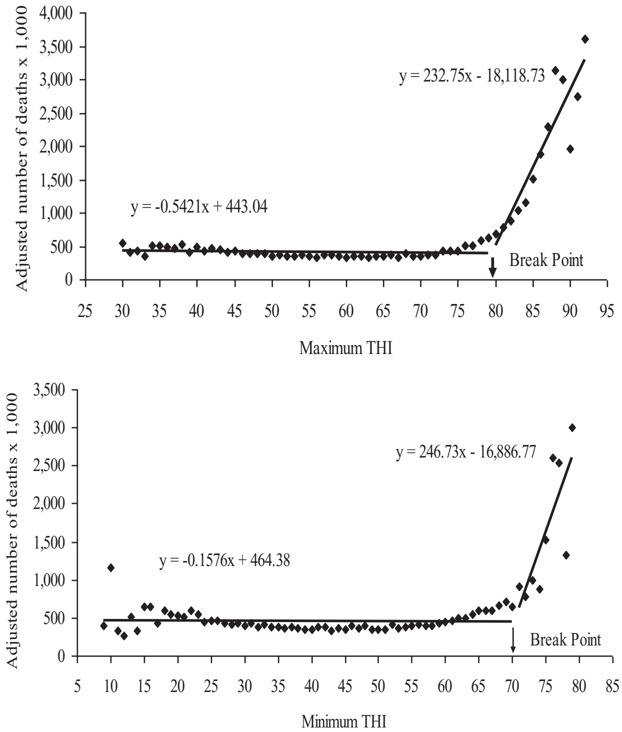

Figure 7. Adjusted number of deaths in relation to maximum (A) and minimum (B) THI; (A) a break point was detected at 79.6 THI. Below the break point, the adjusted number of deaths was constant across THI values ($R^2 = 0.0119$, $F_{1,50} = 0.910$, $P = 0.5$), whereas above 79.6 THI, the adjusted number of deaths rose sharply with THI ($R^2 = 0.8382$, $F_{1,13} = 269.65$ $P \leq 0.001$); (B) a break point was detected at 70.3 THI. Below the break point, the adjusted number of deaths was constant across THI values ($R^2 = 0.0004$, $F_{1,62} = 0.930$, $P = 0.5$), whereas above 70.3 THI, the adjusted number of deaths rose sharply with THI ($R^2 = 0.6151$, $F_{1,9} = 707.01$, $P < 0.001$). From Vitali et al. (2009).

there is considerable opportunity to improve thermal resistance and performance in dairy cattle. These differences include thermoregulatory capability, feed intake and production responses, and cellular differences in heat shock responses (Hansen, 2004; Collier et al., 2006). Studying the relationship between genotype and thermal tolerance offers opportunities for engineering animals that are more resistant to climatic stressors.

Conclusion

A variety of environmental factors such as ambient temperature, solar radiation, relative humidity, and wind speed are known to have direct and indirect effects on domestic animals. The direct effects involve impacts of the environment on thermoregulation, the endocrine system, metabolism, production, and reproduction. Indirect effects include impacts of the environment on food and water availability, pest and pathogen populations, and resistance of the immune system to immunologic challenge. Animals have developed coping mechanisms to minimize the impact of these environmental stressors on their biological systems. These responses are broadly described as acclimation, acclimatization, and adaptation. Acclimation is the coordinated phenotypic response developed by the animal

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to a specific stressor in the environment while acclimatization refers to the coordinated response to several individual stressors simultaneously (e.g., temperature, humidity, and photoperiod). In general, there is hardly ever a case in the natural environment where only one environmental variable changes. Thus, in most cases the animal is undergoing acclimatization to the changing environment. Acclimation and acclimatization involve phenotypic and not genotypic change, and the acclimation responses will decay if the stress is removed. The overall impact of acclimation and acclimatization is to improve the fitness of the animal in the environment. In many cases, the acclimation response is induced by sudden environmental change. In other examples, the acclimation response is driven by changes in photoperiod or other environmental cues such as day length, which permit the animal to "anticipate" the coming change in the environment leading to seasonal acclimation adjustments in insulation (coat thickness, fat deposition), feed intake, or reproductive activity in advance of the actual environmental change. However, in every case, the process is driven by the endocrine system which coordinates metabolism to support a new physiological state, the acclimatized animal.

Acclimatization to a stressor is a two-stage process. The first stage is driven by homeostatic responses to environmental change and the second stage is a homeorhetic process driven by the endocrine system which enables animals to respond to a stress. The resulting cellular, metabolic, and systemic changes associated with acclimatization is to reduce the impact of the stress on the animal and allow it to function more effectively in the stressful environment. These changes are lost if the stress is removed so the process is not based on changes in the genome. However, if the stressful environment is not removed over successive generations these changes will become "genetically fixed" and are referred to as adaptations. A better understanding of genetic differences between adapted animals will contribute useful information on the genes associated with acclimation. Likewise, study of gene expression changes during acclimatization will assist in identifying genes associated with improved thermotolerance.

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Feature Article

The impact of climate change on extensive and intensive livestock production systems

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Implications

- Extensive and intensive livestock production both contributes and is affected by climate change.
- There is considerable pressure on livestock production to deliver, under changing environmental conditions, on an ever-increasing demand for protein in human diets.
- Delivery on the increase in demand will not be possible without drastic changes to both extensive and intensive production.
- These adaptations/changes should contain mitigation components, which will enable the industry to deliver on the production and environmental demands; however, these changes will come at a monetary cost to producers and consumers.

Key words: adaptive changes, animal production, environment, livestock producers, product demand

Introduction

The majority of animal scientists and livestock producers are fully aware and accept that the livestock production sector contributes to factors causing climate change and that in turn livestock production will also be affected by climate change. These effects will be both direct and indirect (Houghton et al., 2001). The impact of climate change on animal production has been categorized as the following: 1) availability of feed in the form of grain, 2) pasture and forage crop production and quality, 3) health, growth, and reproduction, and 4) diseases and the spread thereof (Rotter and Van de Geijn, 1999). In this article, the potential impact of projected climate change on the different livestock production systems (extensive and intensive) will be discussed in general with emphasis on the adaptation aspect. It is, however, important to put the livestock production sector into perspective before speculating on potential future changes.

What do we mean when we talk about livestock production and what is the definition of livestock? It is defined as domesticated animals raised in an agricultural production system with the aim of producing food, fiber, and labor. Sometimes, reference is only made to ruminants, such as cattle, sheep, and goats but this definition should include all livestock which fits the original description, including poultry, pigs, and so on.

Over time the livestock sector has increased in size and relative production output, especially in intensive animal farming practices (Muir, 2011). The increase in intensive beef cattle production in beef feedlots is due to the increasing global demand for protein (Millen et al., 2011; Costa Junior et al., 2012). In Brazil, Costa Junior et al. (2012) reports that the number of beef cattle fed in feedlots has more than doubled since 2012. Verge et al. (2008) ascribe this to the fact that this increase was driven by both population increases and the increased demand for higher rates of protein inclusion in human diets. A positive correlation exists between the expansion of beef cattle enterprises and those for the other species, where the same trend is observed. This increase has also been observed by the IPCC where an estimated 1.4-fold increase in numbers for cattle, buffalo, sheep, and goats, and a 1.6- and 3.7-fold increase for pigs and poultry, respectively, has taken place since 1970s (Smith et al., 2014).

Livestock systems, especially in developing countries, are extremely dynamic and various drivers of change can be identified. This includes increasing populations and incomes which are combining to drive considerable growth in demand for livestock products. This is projected to continue well into the future (Delgado et al., 1999), although at diminishing rates (Steinfeld et al., 2006). A second feature of the growing demand for livestock products is the shift in the location of production. An example of this is the rapid urbanization of (particularly monogastric) livestock production (the landless monogastric production system—LLM systems), followed in time by ruralization again. This second ruralization move is primarily in response to environmental drivers, meaning that after the initial urbanization, the pressures on resources and environmental pollution forces these production systems to less densely populated rural areas again. In addition to the factors associated with the "livestock revolution" (Delgado et al., 1999) and "livestock in geographic transition" (Steinfeld et al., 2006), other drivers may have far-reaching impacts on the livestock sector in the coming decades: the green agriculture movement (organic food, fair trade, etc.) and the increasing importance of fodder crops being grown for biofuel, for example. There may be considerable impacts of climate change on agricultural systems in the future, but it is clear that climate change is only one of several key drivers of change. Other factors such as population

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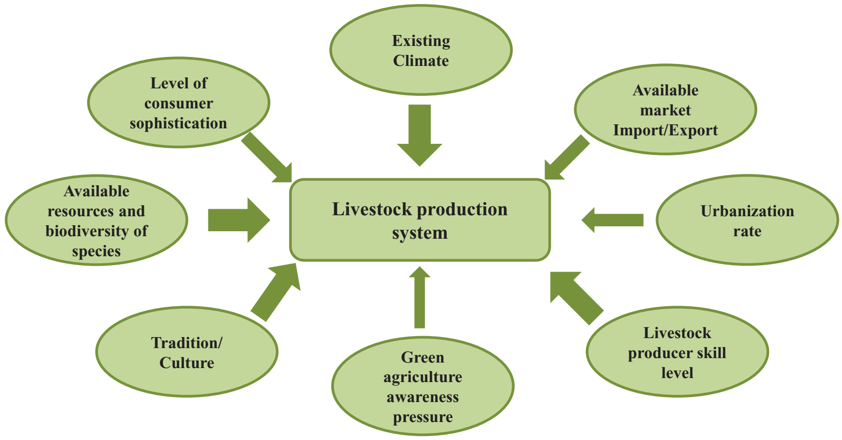

Figure 1. Main drivers of a specific livestock production system *(weight of arrows indicate relative importance)*.

growth, globalization, urbanization, changing socioeconomic expectations, and cultural preferences, for example, may have a considerable impact on the system and on food security. The most important factors influencing a specific livestock production approach can be summarized in Figure 1.

Global livestock production is not uniform. There are differences in livestock production needs between developed and developing countries. These differences even exist within countries where certain areas may favor a certain approach to livestock production. Although both intensive and extensive production systems are practiced in both developed and developing countries, the trend is for production systems to be more intensive in the developed countries as compared with a more extensive approach in developing countries. Knowledge of the distribution of livestock resources can be applied in many ways, for example, in estimating production and off-take, the impacts on the environment, disease risk and impact, and the role that livestock plays in people's livelihoods (FAO, 2007; Robinson et al., 2007). Livestock in different contexts serve quite different functions, play different roles in people's livelihoods, vary in herd structure and breed composition, and are subjected to very different husbandry systems (Robinson et al., 2011).

These differences are mainly driven by internal factors, such as economic development, resource availability, population dynamics and rate of urbanization, culture, etc. (Figure 1).

What Is the Role and Importance of Livestock Production?

It is estimated that grasslands cover approximately 30% of the earth's ice-free land surface and about 70% of its agricultural lands (White et al., 2000; WRI, 2000; FAO, 2005). Livestock, and more specifically ruminants, are still the most effective organisms to convert grass into protein. An estimated 1 billion people depend on livestock, and 70% of the 880 million rural poor are to some extent dependent on livestock for their livelihoods (World Bank, 2007). Livestock production is practiced on two-thirds of global drylands (Clay, 2004). Extensive pastoralism occurs on 25% of global land surface and supports around 200 million subsistence pastoral households (Nori et al., 2005). In Africa, 40% of the land is dedicated to pastoralism (IRIN, 2007) and 70% of the population relies on dry and subhumid lands for their daily livelihoods.

Twenty-three percent of the world's poor (nearly 300 million people) are located in sub-Saharan Africa, and about 60% of these depend on livestock for some part of their livelihoods (Thornton et al., 2002). In sub-Saharan Africa alone, 25 million pastoralists and 240 million agro-pastoralists depend on livestock as their primary source of income (IFPRI and ILRI, 2000). Figure 2 illustrates the global density of livestock.

The type of production systems utilized shows more or less the same pattern, with intensive systems more dominant in the high-density regions and vice versa in the low-density regions.

Livestock products are the main outputs of natural and planted pastures and continue to be the fastest growing agricultural subsector globally. In some developing countries, the livestock sector accounts for 50–80% of GDP (World Bank, 2007). This gives us some indication on how important livestock and livestock production is for the world population and the global economy.

Livestock production is estimated to be responsible for 37% of global anthropogenic (originating from human activity) methane (CH_4) emissions and 65% of anthropogenic nitrous oxide (N_2O) emissions (FAO/LEAD, 2006). Methane from enteric fermentation in livestock is reported to be 85.63 million tonnes while the contribution from manure is estimated to be 18 million tonnes annually (FAO/LEAD, 2006). Of the total methane emissions from enteric fermentation, grazing systems contribute some 35% compared with 64% for mixed farming systems (FAO/LEAD, 2006). This illustrates the "catch twenty two" situation we are in—we are fully aware how detrimental livestock is to the environment but we can't do without them.

What Are the Different Livestock Production Systems?

Livestock production is categorized according to the classification system devised by Seré and Steinfeld (1996; Table 1).

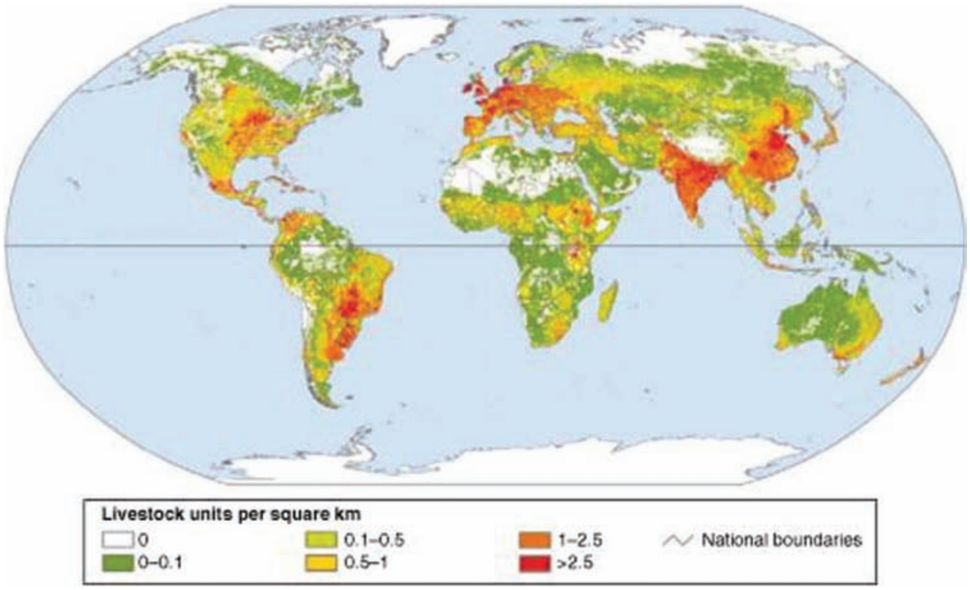

Figure 2. Global density of livestock (units per square kilometer) (FAO, 2006).

This classification system consists of two main criteria, namely agro-climatic and type. Illustration of the components of livestock production systems is shown in Figure 3.

The following definitions apply:

- Agro-climatic criteria—based on the length of growth period (**LGP**). Growth period is defined as the period in days during the year where the available rain fed moisture in the soil is greater than 50% of potential evapotranspiration. Excluded are periods of a mean temp of less than 5 °C.
- Type criteria—whether it is a livestock only system or mixed farming system where a crop production element is included.
  - Arid/semi-arid—LGP of less or equal to 180 days.
  - Humid/subhumid—LGP of more than 180 but less or equal to 270 days.
  - Tropical highlands/temperate—LGP of more than 270 days and month or more with sea level corrected temp of below 5 °C, during growth period the mean temperature is between 5 and 20 °C.
  - Solely livestock—where 90% of dry matter comes from rangelands, pastures, annual forages, and purchased feeds and less than 10% of production comes from nonlivestock activities.
  - Mixed system—more than 10% of dry matter fed to animals comes from crop by-products, stubble, or more than 10% of total value of production comes from nonlivestock farming activities.
  - Grassland-based systems—more than 10% of dry matter is produced on the farm.
  - Landless system—less than 10% of dry matter is produced on farm.
  - Rainfed mixed farming systems—more than 90% of nonlivestock farm production is from rainfed land use.
  - Irrigated mixed farming systems—more than 10% of value from nonlivestock production comes from irrigated land use.
  - Monogastic—value of pig/poultry production is more than ruminant.
  - Ruminant—ruminant production is higher than pig/poultry.

For the purpose of this article, these systems will only be discussed under the two main generic criteria, namely extensive and intensive systems.

How Will Extensive Systems Adapt/Change under a Predicted Climate Change Scenario?

It is suggested that extensive livestock production systems will come under increased pressure with predicted climate change scenarios (Figure 4). The causative factors are in the introduction. The following are predicted adaptive changes to

Table 1. Livestock production systems simplified and coded (Seré and Steinfeld, 1996)

Generic	Specific	Systems
LG (livestock only)	LGA	Livestock only/arid/semi-arid
	LGH	Livestock only/humid/subhumid
	LGT	Livestock only/highlands temperate
MR (mixed rainfed)	MRA	Mixed rainfed crops/livestock/arid/semi-arid
	MRH	Mixed rainfed crops/livestock/humid/subhumid
	MRT	Mixed rainfed crops/livestock/temperate
MI (mixed irrigated)	MIA	Mixed irrigated crops/livestock/arid/semi-arid
	MIH	Mixed irrigated crops/livestock/humid/subhumid
	MIT	Mixed irrigated crops/livestock/temperate
LL (landless)	LLM	Landless monogastric
	LLR	Landless ruminant

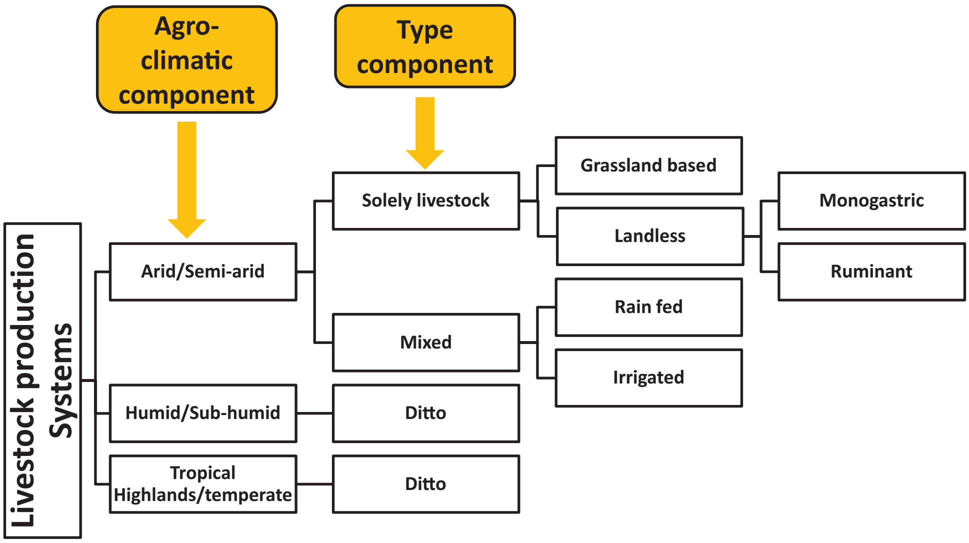

Figure 3. Schematic livestock production classification system.

be made to cope with a changed climatic scenario and to satisfy increased product demand:

- The net effect will in most probability be a slight decrease in the total extent of extensive livestock production systems in both developing and developed countries.
- Spatial movement (extensive livestock production will be practiced in areas and regions where it was impossible before). The flipside of this will be that extensive systems will disappear from areas where it was traditionally practiced.
  - Camps/paddocks will have to be re-designed to allow for:
  - More shaded areas (trees or artificial).
  - More and strategically placed water points.
  - Smaller enclosed areas (camps/paddocks) to allow for less energy expenditure while grazing and visiting water points.
  - Strategically placed solar-powered lighting to enable animals to graze at night/cooler periods of the day and to rest during hotter periods of the day.
- Farming units will increase in size with less animals per area unit.
- Emphasis will shift to conservative stocking rates, pasture conservation, and rainwater harvesting.
- Indigenous/adaptive breeds will dominate but should not be to the detriment of production levels.
- Production efficiency will become paramount:
  - Survivability (disease, heat, and drought tolerance).
  - Reproduction efficiency/fertility.
  - Feed conversion rates.
  - Actual production (kilogram of meat per hectare) on natural or planted pasture utilized.
- Marker-assisted selection will become more relevant for the genetic improvement of extensive production animals.
- Diversification of species will be needed (mixture of small and large stock).
- Small stock species will begin to dominate over large stock species.
- Goats will become a species of choice in some areas due to their grazing/browsing capabilities.
- Pastoralism will come under pressure but might also provide solutions to climate change due to its adaptive nature.
- The production cost of extensive livestock farming will increase to some extent with subsequent increase in product price and potential consumer resistance.
- A relatively high skill set level will be required of extensive livestock farmers to deal with the adaptation/mitigation aspects of climate change.

How Will Intensive Systems Adapt/Change under a Predicted Climate Change Scenario?

It is suggested that intensive livestock production systems will come under relatively less pressure compared with extensive systems. Intensive production systems may actually become the more favored choice. The following are predicted adaptive changes to be made to cope with a changed climatic scenario and to satisfy increased product demand:

- There will be an increase in intensive livestock production.
- Monogastric species will be seen as more "environmentally friendly" and will to some extent displace the current ruminant component.
- Intensive livestock production will move closer to the urban areas (urbanization of the production system) in the near future.
- Housing systems will change considerably with self-sufficient energy supply, air filtration, recycling of water, and sophisticated cooling systems.
- The spatial placement of housing systems will allow for smaller units with fewer animals per unit and be placed in such a way as to enhance biosecurity.
- Ruminant and monogastric diets will become more refined,

Figure 4. An extensive livestock production scenario with a high environmental cost and not effectively contributing to overall production.

keeping in mind the life cycle environmental production cost of the components used.
- Drought tolerant grains will form part of ruminant and monogastric diets as opposed to less drought-tolerant varieties.
- Manure management of intensive systems will become industrial processes to minimize environmental impact and to generate re-usable energy.
- Genetic selection will be leaning toward bigger fast growing animals which will be more efficient under intensive conditions.
- Marker-assisted selection will become essential for the genetic improvement of intensive production animals.
- There will be a shift from extensive to intensive production systems in developing countries.
- Developing countries will increase their share in the total production of animal protein as their resource base still lends itself for the expansion of animal production.
- The production cost of intensive livestock farming will increase considerably with subsequent increase in product price and potential consumer resistance.
- A "very high" skill set level will be required of intensive livestock farmers to deal with the adaptation/mitigation aspects of climate change.

Conclusion

The bottom line is not to attempt to predict the future but rather to have all the relevant data available (both historic and modeled predictions) to make informed decisions. All relevant information should be used by animal scientists, veterinarians, climatologists, and farmers together with trends observed in practice to adjust a specific production system as the situation develops. If predictions are correct, climate change and the effects thereof will be a relatively slow process. It will, therefore, allow time for adjustments to be made to negate the effects of climate change. However, it is advisable not to delay these changes and rather implement them preemptively to buffer and negate the potential impact of climate change. It is, however, true to speculate that regardless if and to what extents climate change will occur, changes will have to be made to our current "way of doing things." This is already demanded by the current and predicted increase in protein consumption with climate change having a confounding effect. These suggested changes will put us in a position to deal with climate more effectively since these adaptive changes also contain many mitigation elements which in turn will create a win-win situation for livestock production in its totality.

About the Author

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Feature Article

Impact of climate change on animal health and welfare

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Implications

- Climate change is expected to exert an overwhelming negative effect on livestock health and welfare. Several studies suggest that the expected increase of air temperatures might reduce the risk of death and improve health and welfare of humans and livestock living in areas with very cold winters.
- The negative effects of climate change on animal health and welfare will be the consequence of combined changes of air temperature, precipitation, frequency, and magnitude of extreme weather events and may be both direct and indirect.
- The direct effects of climate change may be due primarily to increased temperatures and frequency and intensity of heat waves. Depending on its intensity and duration, heat stress may affect livestock health by causing metabolic disruptions, oxidative stress, and immune suppression causing infections and death.
- The indirect effects of climate change are primarily those linked to quantity and quality of feedstuffs and drinking water and survival and distribution of pathogens and/or their vectors.
- Development and application of methods linking climate data with disease occurrence should be implemented to prevent and/or manage climate-associated diseases.

Key words: health, immunity, metabolism, microorganisms, vectors

Introduction

Climate is one of many factors with the potential to alter disease states and is expected to exert an overwhelming negative effect on the health of humans and animals (Rabinowitz and Conti, 2013). In addition, several studies suggested that the increase of temperature might reduce mortality and/or improve health and welfare related aspects in humans and livestock living in geographic areas with cold winters (Ballester et al., 2011; Rose et al., 2015).

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The effect of climate change on animal health may be either direct or indirect (Figure 1) and may be due primarily to changes in environmental conditions, which include air temperature, relative humidity, precipitation, and frequency and magnitude of extreme events (i.e., heat waves, severe droughts, extreme precipitation events, and coastal floods). Although this article focuses on the effects of environmental factors, it should be noted that factors leading to the effects of climate change on health are extremely complex, involving not only environmental forces, but also ecological and social aspects, economical interests, and individual and community behaviors (Forastiere, 2010).

The direct effects of climate change on health include temperature-related illness and death. Indirect impacts follow more intricate pathways and include those derived from the influence of climate on microbial density and distribution, distribution of vector-borne diseases, food and water shortages, or food-borne diseases (Lacetera et al., 2013). The aim of this article is to summarize the current state of knowledge regarding the influence of climate and climate change on the health of food-producing animals.

Direct Effects

The direct effects of climate change on health may be due primarily to increased temperatures and frequency and intensity of heat waves (Gaughan et al., 2009). These effects are mediated by induction of heat stress conditions. Depending on its intensity and duration, heat stress may negatively affect livestock health by causing metabolic alterations, oxidative stress, immune suppression, and death (Figure 2).

Metabolic Disorders

Homeothermic animals respond to high temperatures by increasing heat loss and reducing heat production in their attempt to avoid increased body temperature (hyperthermia). Such responses include an increase in respiratory and sweating rates and a decrease in feed intake. These physiological events may provide a significant contribution to explain the occurrence of metabolic disorders in heat-stressed animals (Figure 3).

Heat stress can contribute to the occurrence of lameness in dairy and beef cows (Shearer, 1999). Lameness in cattle may be defined as any foot abnormality that causes an animal to change

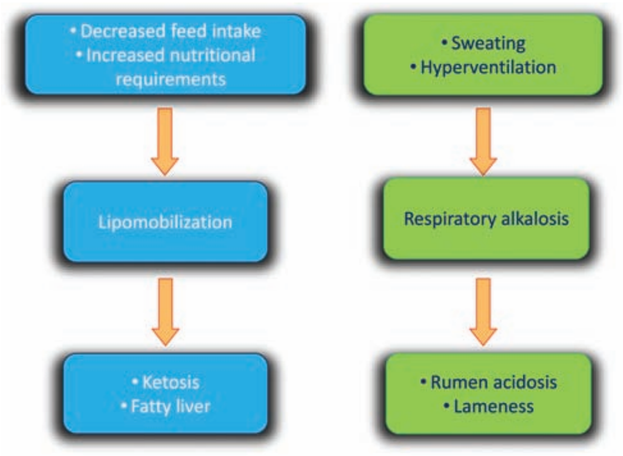

Figure 1. Schematic representation of the impact of climate change on animal health.

the way that it walks. Lameness can be caused by a range of foot and leg conditions, themselves caused by disease, management, or environmental factors and is one of the most significant health, welfare, and productivity issues. The contribution of heat stress to lameness is perhaps due to ruminal acidosis or increased output of bicarbonate (Cook and Nordlund, 2009). Heat-stressed cattle eat less frequently during cooler times of the day, but they eat more at each feeding. Reduced feed intake during the hotter part of the day, followed by increased feeding when the ambient temperature cools down, can cause acidosis which is considered a major cause of laminitis (Shearer, 1999). As ambient temperatures rise, the respiratory rate increases with panting progressing to open-mouth breathing. A consequence is respiratory alkalosis resulting from a rapid loss of carbon dioxide. Cattle compensate by increasing urinary output of bicarbonate. Rumen buffering is affected by a decreased salivary bicarbonate pool. Lameness, with sole ulcers and white line disease, will appear in a few weeks to a few months after heat stress.

The reduction of feed intake combined with increased energy expenditure for maintenance may alter energy balance and explain why heat-stressed animals lose body weight and/or mobilize adipose tissue during heat stress. In particular, during summer, early lactating dairy cows are more likely to experience subclinical or clinical ketosis (Lacetera et al., 1996) and are at higher risk to develop liver lipidosis (Basiricò et al., 2009). Ketosis is a metabolic disease that occurs when the animal is in a severe state of negative energy balance, undergoes intense lipomobilization, and accumulates ketone bodies, which derive from incomplete catabolism of fat. Liver lipidosis is another consequence of the intense mobilization of fat from adipose tissue. Compromised liver function in heat-stressed cattle is testified by reduced albumin secretion and liver enzyme activities (Ronchi et al., 1999).

Oxidative Stress

In farm animals, oxidative stress may be involved in several pathological conditions, including conditions that are relevant for animal production and the general welfare of individuals (Lykkesfeldt and Svendsen, 2007). Oxidative stress results from an imbalance between oxidant and antioxidant molecules and may depend on the excess of oxidant and/or lack of antioxidant substances (Figure 4). In the last 10 to 15 yr, the involvement of heat stress in inducing oxidative stress in farm animals has received increasing interest (Bernabucci et al., 2002; Akbarian et al., 2016). The total antioxidant status concentrations in serum of heifers were lower in the summer than in the winter in peri- and postpartum periods (Mirzad et al., 2018). In mid-lactating cows, plasma values of reactive oxygen metabolite substances were increased during summer. Total carotenes and vitamin E were decreased during summer. Increased oxidant and decreased antioxidant molecules in blood during the hot summer season have been reported both in dairy and buffalo cows. Finally, heat stress has been associated with an increase of antioxidant enzyme activities (e.g., superoxide dismutase, catalase, and glutathione peroxidase), which has been interpreted as an adaptation response to increased levels of reactive oxygen species.

Immune Suppression

The immune system has evolved as a complex of mechanisms to protect the host from invasion by pathogenic organisms. A number of factors may affect the proper functioning of the immune system (Lacetera, 2012). Several studies reported that heat stress may impair the function of the immune system in food-producing animals. Effects of heat stress on immune function are not always straightforward and may depend on the species, breed, genotype, age, social status, acclimation level, and intensity and duration of the exposure to the unfavorable conditions.

Immune suppression facilitates the occurrence of infections, which impairs reproductive efficiency, overall production efficiency, and may compromise animal welfare and increase the

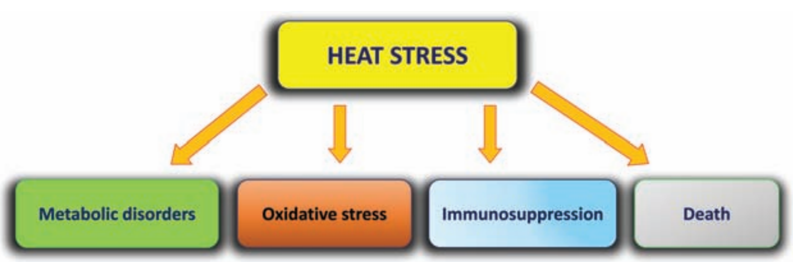

Figure 2. Schematic representation of the most frequent consequences of heat stress on animal health.

use of antimicrobials. Increased use of antimicrobials may lead to development of antimicrobial resistance in microorganisms.

Briefly, Regnier and Kelley (1981) reported that chronic exposure to heat stress impaired immune response in avian species. Nardone et al. (1997) indicated that severe heat stress reduced colostral immunoglobulins (IgG and IgA) in dairy cows with negative consequences on immunization and survival of newborn calves. Lacetera et al. (2005) described a dramatic depression in lymphocyte function in severely heat stressed peri-parturient dairy cows, which may increase their vulnerability to pathogens and also reduce the efficacy of vaccinations. Finally, Lecchi et al. (2016) reported that high temperatures impaired significantly the functionality of neutrophils, which have a central role in the protection of the mammary gland against infections. Mastitis is a major endemic disease of dairy cattle and usually occurs as an immune response to bacterial invasion of the teat canal or as a result of chemical, mechanical, or thermal injury to the cow's udder. Several studies reported the increased occurrence of mastitis during the summer months (Morse et al., 1988; Waage et al., 1998). Results of a recent 2-yr study on the largest Italian dairy farm demonstrated that the greater risk of the occurrence of clinical mastitis in primiparous dairy cows was recorded in July (Vitali et al., 2016). Heat stress may improve the survival capability or growth of pathogens or their vectors (Chirico et al., 1997), and they may surely be involved in these important epidemiological findings. Further epidemiological studies are necessary to determine whether high environmental temperatures are associated with a higher incidence of other infections. The potential for impairment of immune cell function under hot environment supports the use of management practices (i.e., cooling, altered nutritional programs, improved animal hygiene, etc.), which may help to limit the increase of body temperature to prevent outbreaks of infections.

Death

A series of studies have described a greater risk of mortality during the hottest months (Dechow and Goodling, 2008; Vitali et al., 2009) and an increased death rate during extreme weather events (Hahn et al., 2002; Vitali et al., 2015). High temperatures may cause heat stroke, heat exhaustion, heat syncope, heat cramps, and ultimately organ dysfunction. These heat-induced complications occur when the body temperature rises 3 to 4 °C above normal.

In an Indian study, Purusothaman et al. (2008) reported an increase of mortality in Mecheri sheep during summer season. Another series of studies on the effects of temperatures on mortality in farm animals described an increase of deaths during extreme weather events. Hahn and Mader (1997) and Hahn et al. (2002) described the impact on livestock from a weeklong heat wave in the mid-central United States during July 1995. A heat wave is generally defined as a prolonged period of excessively hot weather. It was also reported that during the severe and prolonged heat waves which occurred in Europe during summer 2003, over 35,000 people and thousands of pigs, poultry, and rabbits died in the French regions of Brittany and Pays-de-la-Loire (http://lists.envirolink.org/pipermail/ar-news/Week-of-Mon-20030804/004707.html). Vitali et al. (2015) indicated that summer mortality in dairy cows was greater during days in a heat wave compared with days not in a heat wave. Furthermore, the risk of mortality continued to be higher during the three days after the end of the heat wave. Mortality also increased with the length of the heat wave. Considering deaths stratified by age, cows up to 28 mo old were not affected by heat waves, whereas all the other age categories of cows (29 to 60, 61 to 96, and >96 mo) showed a greater mortality when exposed to a heat wave. The risk of death during a heat wave was higher in the early summer months. In particular, the highest risk of mortality was observed during a heat wave in June.

The temperature–humidity index combines temperature and humidity into a single value and is widely considered a useful tool to predict the effects of the environment on farm animals.

An epidemiological study with dairy cows (Vitali et al., 2009) indicated that 80 and 70 are the daily maximum and minimum temperature–humidity index values, respectively, above which heat-induced death rate increases. In addition, the same study indicated that 87 and 77 are the daily upper critical maximum and minimum temperature–humidity index, respectively, above which the risk of heat-induced death becomes maximum.

A recent study with swine in Italy reported the effects of month, length of the journey, and temperature–humidity index on mortality of heavy slaughter pigs (approximately 160 kg live weight) during transport and lairage (Vitali et al., 2014). The aggregated data of the summer vs. nonsummer months showed

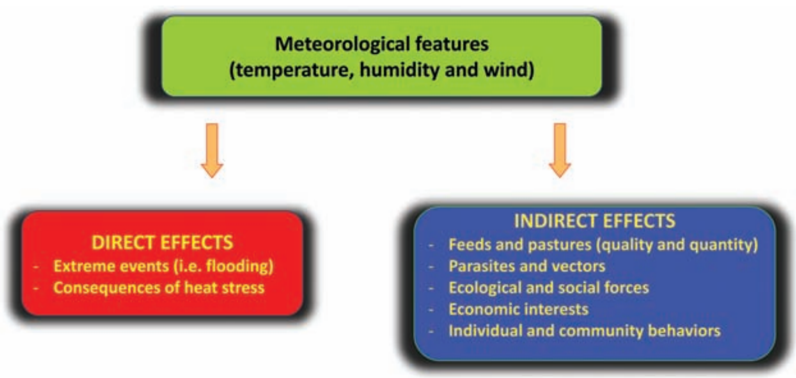

Figure 3. Schematic representation of some mechanisms through which heat stress may cause metabolic disorders in farm animals.

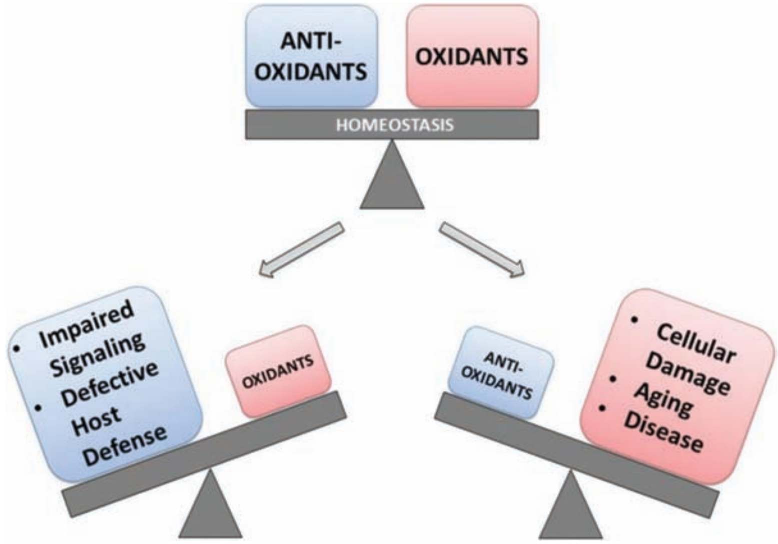

Figure 4. Balance between oxidants and antioxidants molecules in animal health and disease (from Knoefler et al., 2014).

a greater risk of pigs dying during the hot season when considering both transport and lairage. The month with the greatest frequency of deaths was July, whereas the lower mortality risk ratios were recorded for January and March. The mortality risk ratio during transport increased significantly for journeys longer than 2 h. Finally, 78.5 and 73.6 temperature–humidity index were the thresholds above which the mortality rate increased significantly during transport and at lairage, respectively. In a long-term study on scenarios of temperature-related mortality in Europe, Ballester et al. (2011) predicted a change in the seasonality of mortality, with maximum monthly incidence progressively shifting from winter to summer from 1950 to 2100.

Indirect Effects

As already described earlier, weather and climate change are likely to affect the biology and distribution of vector-borne infections. For example, temperature changes, global wind and precipitation patterns, and changes in relative humidity in temperate climates will affect positively the reproduction of insects and, consequently, their population density. Thus, some tropical diseases, especially those transmitted by insects, may probably move from their natural basin of endemic to other countries.

Simulating an increase of temperature values by 2 °C, a model tested by Wittmann et al. (2001) indicated the possibility of an extensive spread of *Culicoides imicola*, which represents the major vector of the bluetongue virus. This virus is responsible for an infectious arthropod-borne disease primarily of domestic and wild ruminants. Infection with bluetongue virus is common in a broad band across the world. Since 1990, this virus has spread considerably due to changing climatic and environmental conditions necessary to support the *Culicoides* vectors.

Another mechanism through which climate change may alter livestock and human health is represented by the favorable effects that high temperatures and moisture may exert on growth of mycotoxin-producing fungi. Growth of these fungi and the associated toxin production are closely related to the temperature and degree of moisture, which are dependent on weather conditions at harvest and techniques for drying and storage of grains (Frank, 1991). Mycotoxins can cause acute disease episodes when animals consume critical quantities of contaminated feeds. These mycotoxins may have a negative effect on specific tissues and organs such as liver, kidney, oral and gastric mucosa, brain, or reproductive tract. Most frequently, however, concentrations of mycotoxin in feeds are below those that can cause acute disease. At low concentrations, mycotoxins may reduce the growth rate of young animals. Some mycotoxins may interfere with the native mechanisms of disease resistance and may impair immunologic responsiveness, making the animals more susceptible to infection (Bernabucci et al., 2011).

Finally, other examples of how climate change may affect animal health are provided from parasitic diseases. In this context, gastrointestinal nematodes are important parasites of livestock, causing mortality and morbidity. Because a significant part of the life cycle of these parasites is completed outside of the host, their survival and development are susceptible to climate change. In this regard, a recent simulation study (Rose et al., 2015) predicted that future climatic data for a temperate region will have an opposite effect on annual infection pressure (increase or decrease) depending on the species of parasites.

Conclusions

Although further epidemiological studies are needed, a significant amount of research has already demonstrated that climate change will affect animal health and welfare. Heat stress conditions as a result of global warming, high air temperatures, and higher frequency of extreme weather events and droughts may negatively affect animal health and welfare. Such effects may take place by direct and/or indirect mechanisms. Tools and techniques for an animal disease surveillance system to incorporate animal data with relevant climate conditions are also needed. Development and application of methodology to link climate data with disease surveillance systems should be implemented to improve prevention of diseases as well as mitigation and adaptation responses of animals to heat stress.

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Impact of heat stress on cow reproduction and fertility

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Implications

- Summer heat stress is a major cause of low fertility in dairy cattle. Consequently, cows are unable to conceive.
- Severe hyperthermia results from high metabolic heat production and low rate of evaporative heat loss. Application of efficient cooling is a must to minimize heat stress.
- Multiple reproductive processes are impaired, including oocyte competence, embryonic growth, gonadotropin secretion, ovarian follicular growth steroidogenesis, development of the corpus luteum , and uterine endometrial responses.
- Treatments combined with cooling may improve fertility. Combinations of GnRH and $PGF_{2\alpha}$ are used to improve fertility. Embryo transfer and progesterone supplementation also improve fertility of subpopulations of cows.

Key words: cooling, cows, fertility, heat stress, ovarian function

Introduction

Hyperthermia in summer

Heat stress during the summer disrupts several reproductive processes, resulting in a pronounced depression of conception rate in dairy cows worldwide. The rise of internal body temperature during the summer is responsible for the impaired reproduction. A major cause for sustained hyperthermia during the summer is high milk production, which continues to rise. The processes of milk synthesis and secretion increase cows' metabolic heat production. For instance, heat production of cows yielding 30 kg/day milk is twice as high as maintenance heat production of nonlactating cows, and that of high milk yielding cows giving 55 kg/day is about three times higher than maintenance heat production.

Maintenance of normal and constant body temperature requires a balance between endogenous heat produced in the body and the amount of heat lost from the body to the environment. When heat production exceeds heat loss, the body temperature rises. Body temperatures of high milk yielding cows located in a wet region were found to start rising exponentially at air temperatures of 26–27 °C. Thus, even a small rise in air temperature, on the order of 1–2 °C, due, for instance, to global warming, may induce severe hyperthermia in dairy cows. This is clearly seen in Figure 1, which demonstrates the depressive effect of summer heat on the conception rate of lactating cows artificially inseminated (**AI**) in the summer months over the last 18 years to as low as 27.7%, compared with 42.6% during the cool winter months. Moreover, the "slightly" more severe conditions during the summers of 2010, 2012, and 2015, about 1.5 °C above average summer air temperatures, further decreased conception by an additional 5% units (Figure 1).

Cooling approaches

The need to use heat-abatement strategies is a result of high metabolic heat production due to high milk yield, but also of the low sweating rate in cows—about 1/4 to 1/3 of that in horses and man. Until the 1980s, cooling was based on blocking direct solar radiation and using ventilation; it did not involve spraying water on the cows. However, these basic means did not prevent hyperthermia, which led scientists in Israel to examine direct wetting of cows' skin to facilitate evaporative cooling. This cooling approach is based on short-term spraying of water followed by its evaporation from the skin by air from fans (Flamenbaum et al., 1986; Berman and Wolfenson, 1992). The sprinkling and ventilation cooling system is commonly used today worldwide for dairy cows in hot/warm climate countries. Efficient cooling requires several cooling windows per day, consisting of cycles of water spraying and ventilation lasting about 30–50 min each. An alternative approach to cooling cows is low-profile cross-ventilation in free-stall buildings. This approach requires closed barns and is based on evaporative cooling of the microenvironment inside the barn. The low-profile cross-ventilation system is used mainly in the United States.

The efficiency of cooling in commercial farms can be conveniently compared by calculating the ratios between summer and winter milk production and conception rates. Calculations demonstrate that efficient cooling management in high ranking farms makes it possible to maintain milk production in the summer very close (98%) to that in winter. However, the ratios

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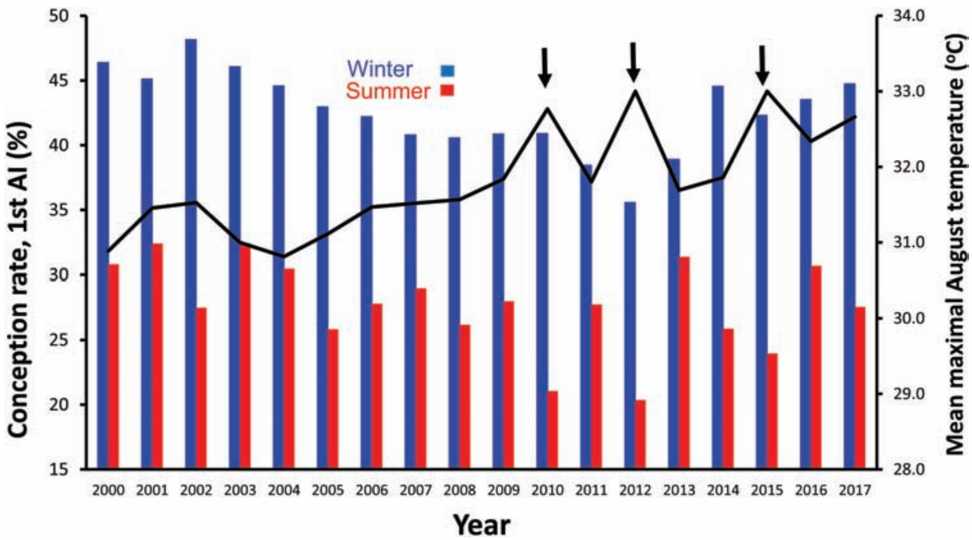

Figure 1. Conception rates in large dairy farms in Israel of cows first inseminated during the winter (January–March) or summer (July–September) of 2000–2017. Mean maximal air temperatures during August month of each year are presented as a black curve. Extreme summer conditions in 2010, 2012, and 2015 are associated with markedly lower conception rates. Adapted from Y. Lavon and E. Ezra, Israel Herd Book, with permission.

also indicate that summer conception reaches 68% of that in winter, much less than the value obtained for milk production. It is thus becoming clear that the reproductive system is highly susceptible to thermal stress.

The economic outcome of seasonal differences in fertility between summer and winter is significant, resulting from uneven milk production throughout the year: excess production in the winter and deficiency in the summer lead to high economic expenses. Furthermore, efforts to achieve a successful conception of cows in summer are also expensive because more AI is required per pregnancy. Other means that may improve conception in summer, based on various hormonal treatments, are described later in this review. Worth noting is that the use of cooling to prevent severe hyperthermia of cows and maintain the smallest possible rise in body temperature is a prerequisite for successful hormonal treatment.

Here, we concentrate on the main processes that are impaired in female cattle and lead to low fertility. The overall scheme of heat stress-induced impairments of reproductive functions is presented in Figure 2. The disruptive effects of thermal stress on male reproduction are beyond the scope of this review.

Gonadotropins

The gonadotropins luteinizing hormone (**LH**) and follicle-stimulating hormone (**FSH**) play important roles in ovarian function, including regulation of follicular growth, ovulation, and corpus luteum (**CL**) development. There is some discrepancy in the literature regarding gonadotropins, but most studies indicate that heat stress depresses LH secretion and compromises its function. For instance, follicle tissues obtained from heat-stressed cows were shown to secrete lower levels of steroids under gonadotropin stimulation (Bridges et al., 2005). Other studies showed lower concentrations of GnRH-induced LH surge under heat stress (Gilad et al., 1993). In another study, decreased expression of LH receptor was reported in the follicles of heat-stressed goats. Reduced LH surge and/or alteration in the sensitivity of follicular cells to LH might, in turn, impair the cascade of events leading to ovulation and formation of a functional CL. Moreover, reduced estradiol concentrations under heat stress in cows close to ovulation may also disrupt the preovulatory LH surge.

Unlike LH, FSH secretion increases under heat stress and is associated with a larger number of follicles growing in the ovaries (Wolfenson et al., 1995). In agreement with this, Roth et al. (2000) showed a pronounced decrease in plasma inhibin concentration in heat-stressed cows, which in turn caused an increase in plasma FSH concentration, known to stimulate follicle growth in the ovaries. These alterations might explain the significant rise of double ovulation and the marked rise in calving of twins following summer insemination.

Low LH surge may cause the development of suboptimal CL secreting low levels of progesterone. Together, altered gonadotropin secretion can depress cow fertility in the summer. A possible approach to "correcting" the situation is to administer a single dose of GnRH at the onset of estrus coinciding with the secretion of the low endogenous LH surge, consequently inducing a normal LH surge. Indeed, studies in which GnRH was administered at the onset of estrus (Kaim et al., 2003) significantly increased conception rates in heat-stressed cows. A single dose of GnRH analogue was administered 2–3 h after onset of estrus. Improvement of conception rate was noted mainly in cows with low body condition, known to have low LH surge. For unclear reasons, the improvement was also recorded in first calving cows, and it was much less pronounced in mature cows (Kaim et al., 2003).

Ovarian Follicles

Cows usually exhibit two follicular waves in a 21-day estrous cycle. In each wave, a single follicle becomes largest and dominant, and the others become atretic and disappear. The dominant

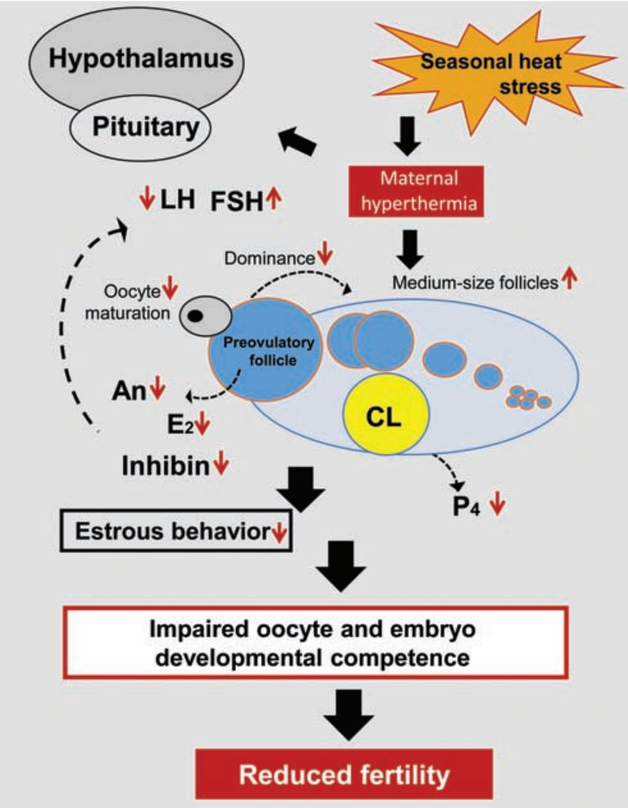

Figure 2. Diagram illustrating the long-term effects of seasonal heat stress on the hypothalamus-pituitary-ovarian axis and its involvement in reducing fertility of lactating cows. Reduced LH secretion is associated with reduced follicular estradiol (E_2) secretion. Reduced dominance of the preovulatory follicle is reflected by reduced androstenedione (An) and E_2 concentrations and is associated with reduced estrous behavior. Increased number of medium-size follicles (6–9 mm in diameter), most likely due to reduced dominance, is associated with reduced inhibin and increased FSH concentrations. Reduced oocyte and embryo developmental competence is associated with disruption of nuclear and cytoplasmic maturation. Reduced plasma progesterone (P_4) concentration is related to impaired function of the CL. Reduced fertility in heat-stressed cows is presumed to result from additive effects. Adapted from Roth and Wolfenson (2016).

follicle of the second wave develops into the preovulatory follicle at the end of the cycle when the endocrine status "permits" induction of ovulation. Heat stress alters follicular growth dynamics in cows. Two physiologically significant impairments associated with attenuation of dominance are worth mentioning here. The first is a rise in the number of large follicles in a follicular wave, which probably underlies the increased numbers of twins following summer inseminations. The second is extended duration of dominance of the preovulatory follicle, resulting from its early emergence (Wolfenson et al., 1995). This finding might explain in part the negative impact of heat stress on fertility because the extended duration of the preovulatory follicle has been shown to be associated with depression of fertility.

A reduction in the steroidogenic capacity of follicles under thermal stress is characterized by less aromatase activity of granulosa cells and decreased estradiol concentration in the dominant follicle (Wolfenson et al., 1997). Figure 3A and B demonstrates lower estradiol production by the granulosa cells in summer vs. autumn and winter, and lower androstenedione production by the theca cells in summer and autumn vs. winter. Seasonal (summer and subsequent autumn) or experimental (5 days of heat exposure in a hot chamber) heat stress had a carryover effect on steroid production (Roth et al., 2001b). Potentially adverse effects of low estradiol production might include impaired estrus duration and intensity; suppression of LH secretion which, in turn, might impair events associated with ovulation; development of ovarian cysts; and alteration of CL functioning, associated with reduced progesterone production (Wolfenson et al., 2000). With respect to depression of estrous behavior in the summer, use of Ovsynch and timed AI protocols have been shown to improve the overall pregnancy rate of cows in summer, most likely because, among other reasons, all of the cows are inseminated, regardless of estrus manifestation (de la Sota et al., 1998). Given the long-lasting effect of heat stress on ovarian follicles, various types of hormonal administration to stimulate follicular growth were tested. Induction of follicular cycles by repeated injections of GnRH and $PGF_{2\alpha}$ eliminated the disruptive effect of heat stress on follicular function. This approach was further developed to improve summer and autumn fertility (Friedman et al., 2011), as discussed further on.

The Corpus Luteum

The CL secretes progesterone, which is essential for embryonic development. Luteal insufficiency refers to the status of a CL that does not secrete adequate amounts of progesterone to support pregnancy, and it has therefore long been associated with low fertility in cows and other female animals. Progesterone supplementation during early pregnancy under nonheat stress conditions improves reproduction to a certain extent; however, findings are controversial because not all studies show a benefit to fertility. Under the conditions of summer heat stress, provision of exogenous progesterone to increase suboptimal endogenous progesterone concentrations may improve conception rate, nevertheless, the benefit of this approach is controversial as well. Studies indicate that in most cases, exposing cows to short-term, acute heat stress is not associated with a reduction in progesterone concentration. The higher concentration of progesterone found in acute type studies has been related to adrenal secretion of progesterone or to the severity of the thermal stress (Bridges et al., 2005). In contrast, a significant decrease of progesterone is typically obtained when cows are exposed to long-term, chronic, seasonal heat stress (Wolfenson et al., 2002). This can be attributed to disruption of the process of CL formation, or to low synthesis of progesterone under hyperthermia, or may be a result of impaired preovulatory follicles which subsequently form a CL with suboptimal function (Wolfenson et al., 2002). The latter possibility is clearly shown in Figure 3C and D, where luteinized granulosa and theca cells obtained from follicles in the summer produced much less progesterone than their counterparts obtained in the winter.

A possible approach to increasing progesterone concentration after insemination in the summer is to insert Controlled

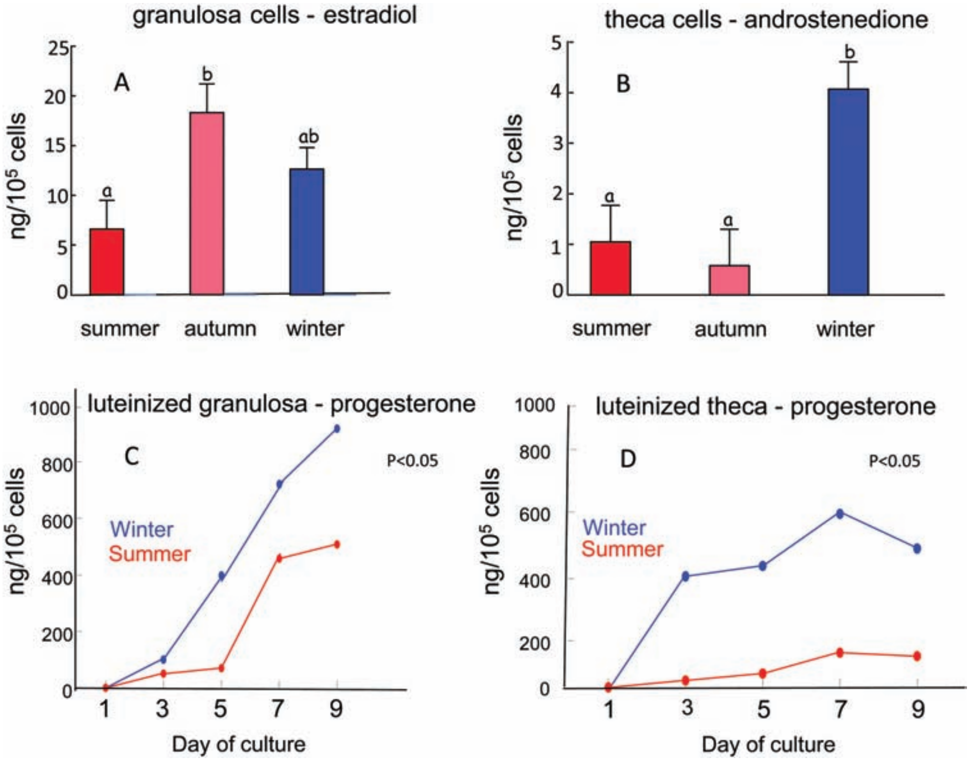

Figure 3. Seasonal differences in steroid production. (A and B) Estradiol production by granulosa cells (A) and androstenedione production by theca cells (B) obtained from dominant follicles on day 7 of the estrous cycle are lower in summer than in winter. (C and D) Progesterone production by luteinized granulosa (C) and theca (D) cells obtained from dominant follicles on day 6 of the cycle is lower in summer than in winter. Cells underwent differentiation to luteal cells for 9 days. Adapted from Wolfenson et al. (1997, 2002).

Internal Drug Release (CIDR) containing progesterone for a period of 2 weeks, starting on day 5 ± 1 after AI. A prerequisite to obtaining a beneficial effect is efficient cooling, otherwise, embryos will not survive. A study by Friedman et al. (2012) showed that CIDR treatment increases conception rate by 6% (not significant); however, the treatment significantly increased the conception rate in subgroups of cows with low body condition after calving, and in cows that exhibited uterine disorders at parturition. Based on the latter, a follow-up study (O. Shiff et al., unpublished data) was conducted in which the CIDR was inserted on day 5 ± 1 after AI only in cows with low body condition after calving or cows diagnosed with uterine disease postpartum. Results confirmed the findings of the earlier study, showing improved conception rate in subgroups of treated cows in the summer. The reasons for the beneficial effect of exogenous progesterone on specific subgroups warrant further research.

The Oocyte

The ovarian pool of oocytes is also sensitive to elevated temperature. A stage-dependent pattern of resistance and sensitivity to heat stress of the follicles and their enclosed oocytes are presented in Figure 4. The oocyte acquires its developmental potential in a stepwise manner during follicular development and therefore, heat stress-induced perturbations in follicular functioning can lead to reduced competence of its enclosed oocyte. Oocytes collected from Holstein cows during the summer exhibited a delay in the two first embryonic divisions (Gendelman et al., 2010). Other studies showed a reduced proportion of oocytes that were fertilized and further developed to the blastocyst stage under heat stress. A period of two to three estrous cycles was found to be required for recovery from summer heat damage and appearance of competent oocytes in the subsequent autumn (Roth et al., 2001a), indicating a long-lasting effect of heat stress on the ovarian pool of oocytes. This might explain the reduced fertility during the autumn, when cows are not exposed to environmental thermal stress. It should be noted that only a subpopulation of the ovarian follicles, rather than the entire follicular reservoir, is damaged upon maternal hyperthermia, reflected by spontaneous recovery of oocyte competence and conception rate during the autumn and subsequent winter. In light of this, enhanced removal of impaired follicles has been suggested to improve fertility (Roth et al., 2001a). In particular, three consecutive follicular waves induced by GnRH and $PGF_{2\alpha}$ during the summer and autumn improved conception rate, mainly in first calving cows and cows with high body condition score postpartum (Friedman et al., 2011). The authors believe that incorporating this approach of enhanced removal of impaired follicles, in subpopulations of cows, will improve, to some extent, the fertility of dairy cows during the summer and autumn.

The mechanism by which heat stress affects the oocytes involves cellular and molecular impairments. Exposing oocytes

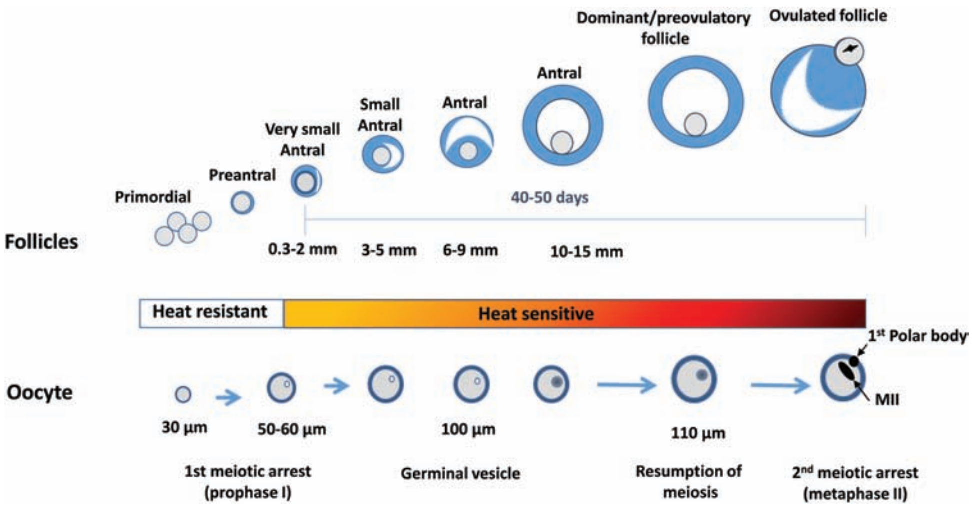

Figure 4. Diagram illustrating stage-dependent pattern of resistance/sensitivity of the ovarian pool of follicles and their enclosed oocytes to heat stress. The primordial, primary, and secondary follicles are heat-resistant, whereas the developing antral follicles, including the dominant and preovulatory follicles, are sensitive to heat exposure with a prominent effect on the germinal vesicle-stage oocyte (developing stage) and metaphase II (MII)-stage oocyte (ovulation). Adapted from Roth (2017).

to heat shock during maturation impaired the rearrangement of their microtubules and microfilaments (Roth and Hansen, 2005), and a high proportion of heat-stressed oocytes were arrested at the metaphase I (MI) stage and had a damaged spindle apparatus. Heat shock of 41 °C reduced the proportion of germinal vesicle stage oocytes that resumed meiosis and progressed to the metaphase II (MII) stage (Payton et al., 2004). Taken together, heat stress-induced alterations in nuclear maturation might be associated with fertilization failure.

A seasonal comparison of mitochondrial distribution indicated a high proportion of category I (i.e., mature) oocytes in the winter, a low proportion in the summer, and an intermediate percentage in the autumn (Gendelman and Roth, 2012). Two potential mechanisms associated with mitochondrial function—apoptosis and oxidative stress—have been documented (for review, see Roth, 2017). Exposing oocytes to 41 °C during maturation increased the proportion of oocytes with fragmented DNA. The expression of apoptotic genes was higher in repeat breeder cows during the summer (Ferreira et al., 2016). Oxidative stress was also suggested to be involved in hyperthermia-disrupted fertility. Exposure of oocytes to heat shock during in vitro maturation increased reactive oxygen species (**ROS**) and reduced the ability of the oocyte to cleave and develop into a blastocyst. Antioxidants have been suggested to overcome the adverse effects of heat stress. For instance, the antioxidant epigallocatechin gallate, the most abundant flavonoid component of green tea, increased the proportion of fertilized oocytes and the percentage of blastocysts in heat-stressed mice.

Heat-induced impairments in maternal transcripts have been shown to underlie the response of the oocyte to heat stress, with further consequences in the developing embryo. Comparison of oocytes collected during the summer and winter revealed differential expression of maternal transcripts (*C-MOS*, *GDF9*, *POU5F1*, and *GAPDH*) involved in oocyte maturation and early embryonic development (Gendelman et al., 2010). The most prominent seasonal variation was a reduction in *POU5F1* mRNA expression in the hot season. Another seasonal study reported the lower expression of genes associated with oocyte maturation (*FGF16*, *GDF9*) in cows during the summer (Ferreira et al., 2016). Another publication reported differential expression of *Cx43*, *DNMT1*, and *HSPA14* in embryos developed from oocytes collected during the summer, relative to those collected during the winter (Pavani et al. 2016).

The Embryo

While much of the effect of heat stress involves alterations in the follicle and its enclosed oocyte, preimplantation embryos are also sensitive to elevated temperature, in a stage-dependent manner (Hansen, 2007). Two-cell stage embryos are more sensitive to heat stress than those at four- and eight-cell stages. Embryos at later developmental stages (i.e., morula, blastocyst) are more resistant to heat stress (Hansen, 2007). Interestingly, heat shock differentially affects embryonic development in different breeds, with a moderate negative effect in *Bos indicus* (Brahman and Nelore) and a larger negative effect in *Bos taurus* (Angus, Holstein).

The mechanism underlying the embryo's acquisition of thermotolerance seems to be associated with changes in the balance between free radical generation and antioxidant protection. In vitro administration of antioxidants (such as anthocyanin and dithiothreitol) protected embryos from heat shock (Sakatani et al., 2007). On the other hand, supplementation of vitamin E, known to have antioxidant capability, failed to improve bovine embryos' tolerance to heat shock. Similarly, supplementation of vitamins A and C did not have any beneficial effect in heat-stressed cows. Treatment of dairy cows with melatonin, a potent ROS scavenger, in the summer before calving, improved their reproductive performance in the subsequent lactation (Garcia-Ispierto et al., 2013).

The balance between pro- and antiapoptotic factors plays an important role in embryonic survival. In cattle, apoptosis does not occur until the 8- to 16-cell stage embryo. Inhibition of heat-induced apoptosis by a specific caspase inhibitor improved embryonic survival. In agreement with this, insulin like growth factor 1 (IGF-I) administration to in vitro-derived embryos improved their resistance to heat shock (Jousan and Hansen, 2007). However, treatment of lactating cows with bovine somatotropin to increase IGF-I concentration did not have any positive effect on pregnancy rate during the summer.

Given that preimplantation embryos at early stages of development are highly sensitive to heat stress, embryo transfer at day 8, to bypass the thermosensitive developmental stages, has been suggested (Hansen, 2013). Embryo transfer during the summer increased pregnancy rate to those achieved with AI or embryo transfer in the winter. It is worth noting that pregnancy rate following embryo transfer can be compromised when the recipient cows cannot maintain normothermia (Vasconcelos et al., 2006), suggesting that the extent of the blastocyst's thermotolerance is limited.

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Conclusions

The reproductive tract, in particular, the ovarian components (i.e., follicles, oocytes, CL), and preimplantation embryos are highly sensitive to elevated temperatures. The authors believe that using an efficient cooling system to maintain normothermia in cows is a prerequisite to any additional remedial approach; body temperature of the recipient cows is critical during embryo transfer; hormonal treatments to support CL function and embryonic survival are more efficient if the cow maintains normal body temperature. Given that the effect of heat stress on fertility is multifactorial in nature, a combination of treatment approaches might be most effective.

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Feature Article

Impact of heat stress on milk and meat production

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Implications

- In recent years, global warming is a major concern for the agricultural sector.
- Heat stress impairs welfare and productive performance of dairy and beef cattle.
- Different climate conditions have important effects on the organic and inorganic components of milk.
- Heat stress in beef cattle is detectable by homeostatic mechanisms (panting, sweating, and urination) and behavioral alterations such as a reduction in activity, increased water intake, and reduced feed intake.
- Global warming will have significant economic impacts for producers and consumers.

Key words: cattle welfare, climate change, growth performance, heat stress, milk quality

Introduction

Global warming is a major concern during recent years, and the livestock sector will be one of the most affected segments of the agricultural industry. However, the effects of increasing temperatures on livestock will be different worldwide, based on latitude and farming systems. In addition to the direct effects of heat stress on animal productivity, global warming will also affect soil fertility, water availability, crop yield, and pathogen circulation (Thornton et al., 2009; Nardone et al., 2010). Therefore, in addition to the arid and tropical areas where heat already represents a major constraint, the most affected areas will be those of the subtropical–Mediterranean zones, which are exposed to considerable heat stress for 3 to 5 mo per year (Silanikove, 2000). Other critical factors in these areas are linked to intensive production systems, which are characterized by high farm animal density of high-producing selected breeds and managed in specialized farms. However, the pasture-based system is equally at risk mainly due to the indirect effects of climate change on pasture growth and water availability (Nardone et al., 2010).

Exposure to uncomfortable thermal conditions (due to the combination of high temperature and humidity) overcomes the capacity of cattle to dissipate heat and leads to an increase in body temperature that exceeds the physiological limits (Ronchi et al., 1997). Such condition is called heat stress and impairs the welfare and productive performance of dairy and beef cattle. In this condition, efficiency of nutrient conversion to energy reduces dry matter intake and increases water consumption, and there is a reduction of efficiency in nutrient absorption. In this scenario, cattle performance worsens rapidly (Collier et al., 1982). To evaluate the simultaneous effect of temperature and humidity factors and to assess the risk of heat stress in cattle, the temperature–humidity index is used.

In the case of dairy cows, climate change has an important effect on milk organic and inorganic composition (Mariani et al., 1993, 1998). Climate change also influences the efficiency of cheese manufacturing processes (Sommerfeldt and Baer, 1986), both on cheese yield and on quality and especially for those cheeses produced using raw and not standardized milk.

Heat stress in beef cattle is usually considered less severe than in dairy cattle because beef cattle have a higher average temperature–humidity index threshold due to their lower metabolic rate and lower body heat production (St-Pierre et al., 2003; Nardone et al., 2010). However, beef cattle also will compensate for increased body temperature by homeostatic mechanisms (panting, sweating, and urination) and behavioral alterations such as reduced activity, increased water intake, and reduced feed intake, which will take place preferentially during the coolest hours of the day (Magrin et al., 2017; Marchesini et al., 2018). The changes in feeding behavior will reflect on the efficiency of rumen function up to the onset of metabolic disorders such as ruminal acidosis (Marchesini et al., 2018). The main consequences are generally lower growth rate and reduced fertility of both males and females (St-Pierre et al., 2003).

The economic losses due to heat stress were estimated by St-Pierre et al. (2003) for the major livestock industries in the United States. In the dairy and beef industries, heat stress had a negative economic impact of $897 million and $369 million per year, respectively. Therefore, this article focuses on the main aspects linked to the effects of heat stress on dairy and beef production.

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The Effect of Heat Stress on Milk Production and Quality

Milk Production

The daily milk yield is highly affected by climate change. The increment of temperature and humidity leads to a significant decrease in milk production (kilogram per day), and this reduction can be easily calculated using the formula proposed by Berry et al. (1964):

$$\text{Decline in milk production (kg / d)} = -1.075 - 1.736 \times \text{NL} + 0.02474 \times \text{NL} \times \text{THI}$$

where NL is the normal level of daily milk yield (kilogram per day), recorded in the temperature range of 10 to 18 °C, and THI is the daily mean temperature–humidity index.

Using this formula, it is clear that daily milk yield (kilogram per day) decreases with the increase of the temperature–humidity index (from 72 to 80), particularly in the more productive cows (from 15 to 40 kg/d). This is even more evident if the decline in milk yield is assessed as percentage of loss (Figure 1). When temperatures move out of the thermo-comfort zone, dairy cows begin to experience heat stress and start to reduce daily milk yield, not because of reduced intake. Accordingly, Cowley et al. (2015) reported that cows subjected to heat stress reduced their ingestion and produced less milk when compared with cows raised in normal climate conditions. In contrast, when cows were fed the same quantity of feed ingested by the heat-stressed group but were not subjected to any heat stress, the decrease in milk production was not significant. In addition, when cows returned to the thermo-comfort zone, milk production increased to the physiological level (Figure 2). To give a practical quantitative evaluation, Bernabucci et al. (2010) reported a loss of 0.27-kg milk per each temperature–humidity index unit incremental change.

Fat Content

The effect of heat stress on milk fat content is not clear, and controversial results have been reported. Abeni et al. (1993) found lower values of milk fat content when the temperature–humidity index value was higher than 75 (3.46 g/100 g for temperature–humidity index < 75 vs. 3.17 g/100 g for temperature–humidity index > 75, respectively). Bernabucci et al. (2015) reported a marked and significant decrease of milk fat during summer (3.20 g/100 g) compared with the values observed in winter (3.80 g/100 g) and in spring (3.61 g/100 g). Also, Summer et al. (1999) observed a decrease in milk fat content during summer when compared with autumn, ranging from a minimum in June–August (3.36 to 3.38 g/100 g) to a maximum in November (3.67 g/100 g). On the contrary, Cowley et al. (2015) did not find any significant differences for milk fat content between cows in normal conditions or subjected to heat stress.

Lactose

Milk lactose, the main component of milk after water, is not affected by heat stress of cows. This is confirmed by Abeni et al. (1993) that found milk lactose content not significantly different between cows maintained at temperature–humidity index < 75 and cows maintained at temperature–humidity index > 75 (5.06 vs. 5.10). This result was confirmed also by Cowley et al. (2015).

Protein, Casein, and Casein Fractions

There are two groups of proteins in milk, caseins, and whey proteins, which are defined by their chemical composition and physical characteristics. Cow's milk, like that of other ruminants, is rich in caseins and comprises about 77% of total milk protein. Among the various factors involved in the cheese-making process, the role of the protein fraction composition and its seasonal changes for milk coagulation to cheese is globally recognized.

When cows are maintained in conditions of heat stress, both milk protein and casein content tend to decrease. Abeni et al. (1993) reported a decrease of milk protein content when the temperature–humidity index value was higher than 75 (3.02 g/100 g for temperature–humidity index < 75

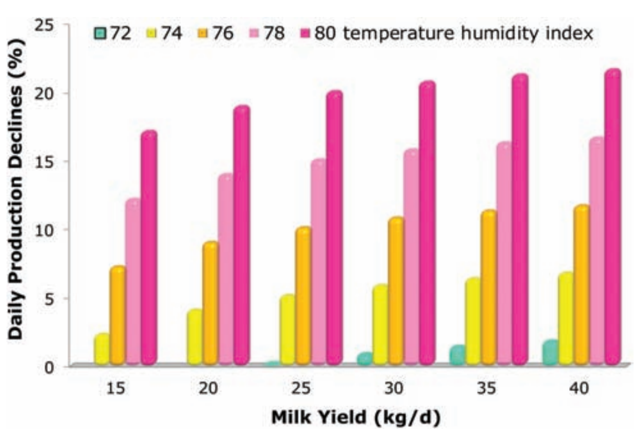

Figure 1. Daily production declines (%) at the increase of temperature–humidity index (Berry et al., 1964).

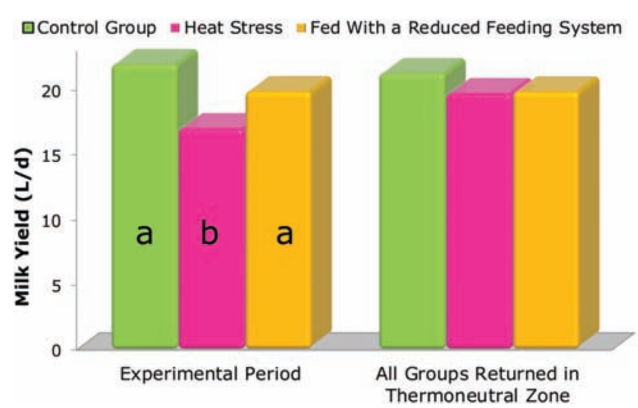

Figure 2. Effect of heat stress and restricted intake (fed with a reduced feeding system) on milk yield. a–b Different letters within period indicate significant differences between treatments ($P < 0.01$; Cowley et al., 2015).

vs. 2.89 g/100 g for temperature–humidity index > 75, respectively). Cowley et al. (2015) found that cows exposed to heat stress produced milk with less protein than cows housed in comfortable temperature conditions. When cows were fed with a reduced feeding system but were not subjected to heat stress, milk protein showed intermediate values. These results suggest that the decrease of milk protein content is mostly related to a direct effect of heat stress instead of a reduction of feed intake.

Regarding milk casein content, Cowley et al. (2015) found differences between cows raised in comfortable temperatures and the heat-stressed group (28.1 vs. 26.8 g/L, respectively). Milk casein content produced by cows fed reduced amounts of feed (but not heat stressed) was statistically different from that of heat-stressed cows, but not from that of cows raised in comfortable temperatures. This suggests that a reduction of milk casein in the heat-stressed group is due to a direct effect of heat stress and that daily feed intake does not affect milk casein content. In accordance, Bernabucci et al. (2015) found higher milk casein content in winter (2.75 g/100 g) and spring (2.48 g/100 g) with respect to the summer season (2.27 g/100 g).

Milk casein is constituted by several fractions, named α_{s1}, α_{s2}, β, κ, and γ caseins. The effect of heat-stressed cows on milk casein fractions and their distribution was investigated by Cowley et al. (2015). For those cows subjected to heat stress, an increase of α_{s1} casein and a decrease of α_{s2} casein was observed. The other fractions do not exhibit any difference between groups of cows. Bernabucci et al. (2015) found that milk produced in summer was lower in terms of α_s caseins ($\alpha_{s1} + \alpha_{s2}$) and higher of κ casein with respect to the other seasons, whereas β casein was similar. These results could lead to changes in the technological properties of caseins and to a different ability to make cheese.

Minerals, pH, and Titratable Acidity

Less is known about the impact of cow's heat stress conditions on milk mineral content and its distribution. Mariani et al. (1993) found significant seasonal variations on the mineral content of milk. These authors observed lower content of milk ash and phosphorus during summer that could be related to the heat stress conditions of cows. Phosphorus has an important role in cheese making, and in some studies, a decrease in phosphorus was related to a worsening of enzymatic milk coagulation.

The climatic conditions in which cows are housed can also affect milk pH and titratable acidity. A correct milk pH, with values around 6.65 to 6.68, and a good milk titratable acidity (the amount of acid compounds in milk), with values from 3.20 to 3.80°Soxhlet-Henkel/100 mL, are essential for an efficient cheese-making process, for high yields of cheese, and for the production of high quality cheeses. Abeni et al. (1993) reported an increase in milk pH and a decrease of titratable acidity when cows were reared at temperature–humidity index values higher than 75. This shows a worsening of these indicators with negative consequences on the production of cheese.

Summer et al. (1999) reported minimum values of milk titratable acidity in August (3.18°Soxhlet-Henkel/100 mL) and maximum values in December and January (3.34 and 3.33°Soxhlet-Henkel/100 mL, respectively).

Milk Coagulation Properties

Rennet coagulation depends on milk composition and quality. Titratable acidity also has a fundamental role. Casein content and milk salt equilibria (contents of calcium and phosphorus and their repartition between the soluble and colloidal phases) are highly important for this enzymatic process. These factors are particularly important for the Protected Designation of Origin cheeses, especially for long ripened cheeses.

Milk coagulation properties are measured by a lactodynamograph, which previews the addition of a determinate quantity of rennet to 10 mL of milk. At the end of the test, a bell-shaped trace is obtained, from which three coagulation traits are obtained: rennet clotting time, which is the time in minutes between rennet addition and the beginning of milk coagulation; curd firming time (k_{20}), which is the time in minutes between the beginning of coagulation and the moment when the bell reaches 20 mm in width; and curd firmness (a_{30}), which is the width (millimeter) of the graph at the end of the 30-min analysis.

Climatic conditions in which cows are housed significantly affect milk coagulation properties. This result is expected because of the strict relationships between coagulation properties and casein content, titratable acidity, and mineral content. The effect on rennet clotting time is marked. Abeni et al. (1993) reported an increased (negative) clotting time when the temperature–humidity index was higher than 75. This result was confirmed by Mariani et al. (1994) that observed the maximum values for clotting time in July (18.97 min) and August (19.42 min) and the minimum in January (15.73 min). In addition, curd firming time is significantly higher when cows are subjected to heat stress. Abeni et al. (1993) observed an increase of curd firming time when the temperature–humidity index value was higher than 75. In the case of a_{30}, Abeni et al. (1993) found lower values of curd firmness when the temperature–humidity index value was higher than 75. This result was confirmed by Bernabucci et al. (2015) that found a significant decrease of curd firmness from winter (35.93 mm) and spring (33.60 mm) with respect to summer (21.98 mm). Summer et al. (1999) reported the monthly variation of all the three coagulation traits. In Figure 3, the trends exhibit the increase of clotting time and curd firming time during July and August and a marked decrease of curd firmness during the same months (minimum value of 10.2 mm in August).

Mariani et al. (1994) found during summer months (July and August) the lowest frequency of milk samples with good or discrete coagulation characteristics and the highest frequency of milk samples with bad or anomalous coagulation characteristics. In particular, in August, milk samples with anomalous characteristics reached 10.58% of total analyzed samples. In the same month, milk samples with good coagulation characteristics exhibited the minimum value of 48.69% with respect to the total analyzed samples.

The response of cows to heat stress is not the same in all breeds. In fact, Malacarne et al. (2005) reported that milk from Italian Friesian cows has a curd firmness value constantly lower than milk from Italian Brown cows (Figure 4). This is due mainly to genetic improvement, particularly on k-casein variant B that was selected in Italian Brown cows. Both breeds showed a decrease during summer, but this decrease was more pronounced for milk from Italian Friesian cows, whereas the value registered for Italian Brown, although lower than values registered in winter and autumn for the same breed, is not different by the value registered in spring.

Somatic Cells

Milk somatic cells are mainly leukocytes; they increase in milk as a response to an inflammation or infection in the cow's mammary gland. Heat stress of cows seems to not have any impact on milk somatic cells. Abeni et al. (1993) found that a temperature–humidity index higher than 75 did not affect the production of milk in terms of milk somatic cell content (logSCC 5.12 for temperature–humidity index < 75 vs. 5.31 for temperature–humidity index > 75, respectively). Regarding seasonal variation, both Bernabucci et al. (2015) and Summer et al. (1999) reported an increase of somatic cell content in summer with respect to winter and spring seasons. In fact, if we look at the analyses of milk produced in northern Italy, the content of somatic cells increases in summer.

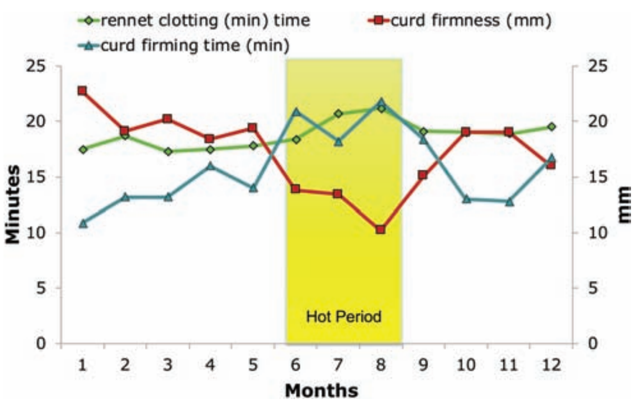

Figure 3. Months of production and Rennet coagulation properties of the milk (Summer et al., 1999). General significance of differences between months was $P < 0.0001$ for all three traits.

Cheese Yield

The characteristics of milk quality produced by cows housed in heat stress conditions lead to a worsening of cheese yield (the amount of cheese obtained by 100 kg of milk). Mariani et al. (1995) reported seasonal variations of Grana Padano cheese yield at 24 h and observed minimum values during the months of July and August, whereas the highest cheese yield was found in the months of October and November (Figure 5).

The Effect of Heat Stress on Beef Cattle

The adverse effects of heat stress on beef cattle are seen at higher temperature–humidity index compared with dairy cattle. These differences are due to breeds characteristics, production, metabolism, feeding plans, and management systems. In fact, the higher threshold temperature for beef cattle is set at 30 °C with relative humidity below 80% and 27 °C with relative humidity above 80% (SCAHAW, 2001). In contrast to dairy cows, the impact of heat stress on the beef sector is not immediately measurable because it does not reflect on a daily production metric such as milk and may vary depending on several factors. These factors, which will be discussed below, can be summarized by breed, stage of production (e.g., beef cows vs. growing/finishing animals), and production system. Regardless of the cattle category and the production systems, heat stress impairs primarily animal welfare.

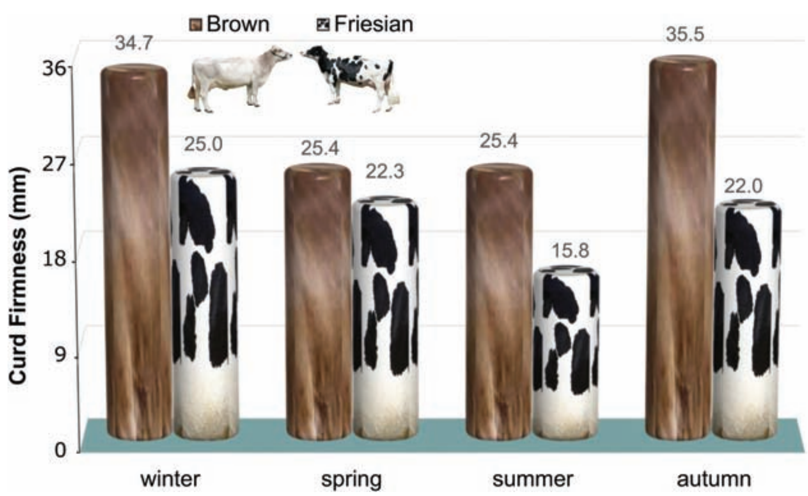

Figure 4. Seasonal trends of curd firmness (millimeter) of Friesian and Brown herd milk (Malacarne et al., 2005).

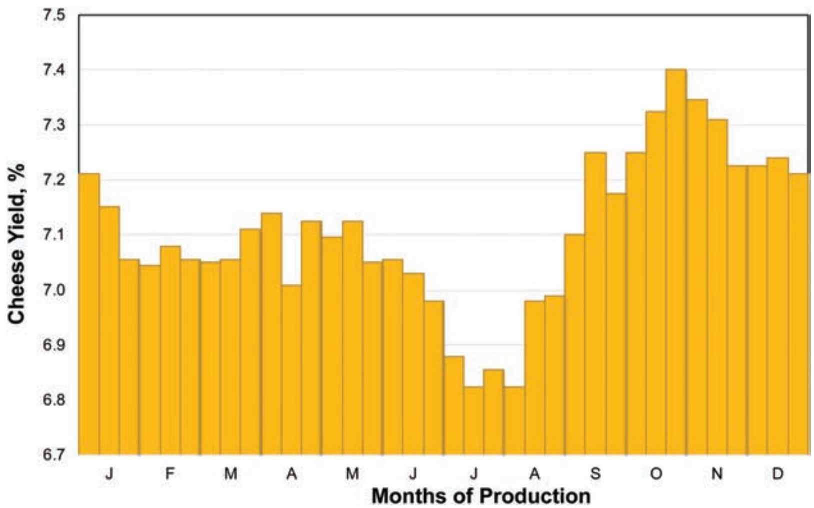

Figure 5. Month of production and Grana Padano cheese yield (%; Mariani et al., 1995).

Welfare Concern

As in dairy cows, heat stress in beef cattle is associated with a higher risk of mortality (Thornton et al., 2009). A study by Morignat et al. (2015) found a pooled mortality risk associated with a 1 °C increase above the hot threshold of about 5% for beef cattle. Moreover, the negative effects of heat stress on animal welfare can be observed by changes in animal behavior, which include higher respiratory rates and panting scores, decreased rumination period, and higher frequency of drinking. Affected animals are also more inactive, spend less time eating (especially during the daylight hours), and less time in social interactions (Brown-Brandl et al., 2006; Magrin et al., 2017; Marchesini et al., 2018). These aspects will invariably lead to production losses.

Cattle Breed

Based on their evolutionary history, different cattle breeds can cope with heat stress with different magnitudes. For example, there is evidence that Braham cattle (*Bos indicus*) can better endure thermal stress than *B. taurus* cattle (Gaughan et al., 2010). Within subspecies, different breeds of *B. taurus* cattle have different levels of heat tolerance. At this regard, a study by Pereira et al. (2014) demonstrated that Limousine cattle cope better with thermal stress and limit the increase in body temperature with lower thermoregulatory reactions than Holstein Friesians. When Limousine is compared with two local Portuguese breeds (Alentejana and Mertolenga), they performed equal to Alentejana and better than Mertolenga in maintaining body temperature stability. Moreover, fatter animals and/or with a heavier hair coat (i.e., higher insulation) and/or darker coated animals (e.g., Angus) are more sensitive to heat (Brown-Brandl et al., 2006; Nardone et al., 2010).

Stage of Production

The beef cattle sector includes the breeding herd and growing/finishing phases, as well as bulls and heifers, which are generally raised in different locations, with different management practices and sometimes even in different countries (e.g., breeding herds in France and finishing units in Italy). Therefore, the impact of heat stress also differs between the two cattle categories (nursing/breeding cows and growing animals) affecting mainly the reproductive sphere in the case of the cows, and the carcass yield in the case of the beef, without prejudice to the welfare issue in both cases. Regarding the breeding beef cows, the magnitude of the production losses could be relatively small when the breeding season (as traditionally occurs) coincides with a period of low heat stress as in the spring (St-Pierre et al., 2003). The same could happen in the case of finishing beef when the stressful thermal conditions last for a relatively short period and are followed by sufficient time for the animals to recover by compensatory gain. However, it was demonstrated that beef cattle under heat stress had lower growth rates and, when slaughtered during or immediately after this period, had lower carcass weight, lower fat thickness, and worse meat quality in terms of pH, tenderness, and color (Mitlöhner et al., 2001; Nardone et al., 2010; Marchesini et al., 2018).

Production System

Worldwide, beef cattle are usually raised outdoors and exposed to natural climatic conditions, whereas only a small portion of them are raised in closed housing systems (Nardone et al., 2010). In general, there are three main beef production systems: pasture based (mainly breeding cows), finishing in outdoor feedlots, and finishing in indoor systems. Depending on the system, different factors can influence the occurrence of heat stress in beef cattle.

The pasture-based system is generally adopted for breeding cows, which are maintained under semi-natural conditions, being on pasture from at least spring to autumn (Nguyen et al., 2010). This semi-extensive system allows the animals to freely adopt coping strategies with weather conditions. These animals usually have some access to shade from trees and the possibility to seek water and air movement to cool themselves (Magrin et al., 2017).

The feedlot is an outdoor intensive system in which the factors that enhance heat stress are the confinement of cattle in restricted areas that prevent some of their natural coping behaviors (e.g., migration to cooler areas, seeking the protection of shade, etc.) and the high-energy feeding plan. Therefore, specific measures to mitigate heat stress in finishing beef systems are needed, with regard to feed management and pen facilities. Beneficial effects were reported with the use of restricted feeding plans and ad hoc bunk management that concentrated the feed distribution in the evening and kept the bunks empty during the hottest hours of the day (Mader, 2003). Regarding pen facilities, good results were given by sprinkling cattle or pen surfaces and providing shade (Mitlöhner et al., 2001; Mader, 2003; Nienaber and Hahn, 2007).

The indoor finishing system (Figure 6) is largely adopted in Europe, where cattle are often imported from neighboring countries. In this system, young beef cattle coming from pasture-based systems arrive after long trips in a truck and are housed in roofed facilities where they are kept on fully slatted floors or on deep litter (Cozzi et al., 2009). In this case, direct sun radiation is prevented, but animals face other challenges linked to the change in climate conditions and indoor confinement. In fact, besides the extreme temperature–humidity index conditions, cattle are particularly vulnerable to rapid changes in environmental conditions (Nardone et al., 2010). Therefore, factors that can influence heat stress in the indoor finishing systems are the high-energy feeding plan (as in the feedlot) and the environmental and micro-climate conditions of the barns. Hence, heat mitigation strategies in this

Figure 6. Italian indoor beef cattle housing system.

Figure 7. Ceiling fan for the control of the temperature in barns. The fan is fitted with five or six aluminum blades. The diameter of the fan varies from 3 to 5 m depending on the size of the barn.

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Andrea Summer is professor of Animal Science in the Department of Veterinary Science at the University of Parma. His main research focuses on the influence of genetic factors on milk quality and milk cheese-making properties, effect of somatic cell counts on milk qualitative characteristics, and the role of minerals in cheese-making. He also characterized milk from different species such as yaks, horses, donkeys, and wild ungulates. He is an expert in the production of Parmigiano-Reggiano cheese and is a member of the control committee of its production. He coordinates the laboratory "Quality of Milk and Dairy Products" at the University of Parma. He is President of the Mastitis Council Italia and of the Italian Dairy Science Association and a member of the Italian International Dairy Federation. **Corresponding author:** andrea.summer@unipr.it

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Flaviana Gottardo is professor of Farm Animal Husbandry and Welfare at the University of Padova, Department of Animal Medicine, Production and Health. Her research focuses on farm animal behavior and welfare. She studies optimization of management systems to improve the welfare of dairy and beef cattle and pigs and monitors animal health and welfare at the farm and at the slaughterhouse. She is a scientific coordinator of several national projects and she is the scientific leader of University of Padova research group partner within European projects (Horizon 2020 and Susan EraNet).

Paolo Formaggioni graduated in Chemistry and later in Food Science and Technology at the University of Parma. He obtained a PhD in Animal Production, Quality and Food Safety from the University of Parma. Since 1998, he has been characterizing milk for cheese making with particular reference to the protein and mineral components of milk. Since 2015, he has been teaching the course "Parmigiano Reggiano Cheese" at the University of Parma. He is a member of the Scientific Secretariat and of the Editorial Committee of the scientific journal, *Scienza e Tecnica Lattiero-Casearia*.

case include changing the feeding plan (as previously discussed for outdoor feedlots), providing adequate water supply (possibly by additional water stations), and adoption of cooling systems, such as ventilation. Large ceiling fans (Figure 7) gave good results by improving animal welfare, health, and performances and by improving litter (and air) quality due to their ability to increase the circulation of air and dry out the litter (Magrin et al., 2017; Marchesini et al., 2018). Water sprinkling or misting is usually not recommended for indoor systems, as it would increase the slipperiness of slatted floors and the wetness and dirtiness of the deep litter, with negative consequences for the animals. Moreover, misters or sprinklers could limit the efficiency in which animals dissipate heat, especially in cases of already high relative humidity (Magrin et al., 2017).

Conclusions

Heat stress has considerable effects on cattle welfare and production. In hot and humid climate conditions, dairy cows produce less milk with lower milk quality characteristics, especially those related to cheese-making. In beef cattle, heat stress impairs reproductive performance of nursing cows, decreases growth rate, and worsens meat quality in growing/finishing animals.

In view of the current climate changes, therefore, we need to cope with the increase in global temperature that threatens to affect cattle-derived food production. Consequently, to maintain the quantity and quality of milk and meat products, it will be necessary to modify management systems to adapt to the new climatic conditions. Management options include acting at different levels such as the feeding plan, the selection of resilient animals, and adoption of technological tools (heat mitigations systems, automated systems for feed distribution).

However, adaptation to the new environmental conditions will not be inexpensive because it will require a greater expense in terms of energy consumption (in the indoor, intensive, finishing systems) or lower production (especially in pasture-based systems) due to the restriction of available feed and water resources. Therefore, the effort for maintaining good animal welfare conditions and acceptable levels of production and quality will inevitably reflect an increase in production costs per kilogram of end product.

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Feature Article

Adaptation strategies: ruminants

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Implications

- Growing populations and reduced access to arable land mean that animal production systems will either need to intensify and/or produce more from a reducing land and other resource base.
- Variable and unpredictable environmental conditions mean that animal production faces numerous challenges. In addition to climate, these challenges include increased disease risk, increased nutritional deficiencies, and lack of capital to support diversification.
- Predicted changes in climate will impose selection pressures on traits important for biological fitness (and production).
- Genetic adaptation is important for the future of livestock systems. Animal adaptation involves trade-offs, which must be considered when selecting animals for use in breeding programs.

Key words: adaptation, constraints, mechanisms, ruminants

Underlying Problems

Why do animals need to adapt? What are the issues that need to be addressed (e.g., poor fertility, nutritional challenges)? These are the important questions livestock producers and animal scientists face. Animal adaptation is a function of a number of intertwined factors (i.e., animal × management × resources). Animal adaptability is as much about the animal as it is about the adaptability of caretakers and their use of available resources (e.g., land, feed, water, and capital). Any discussion about animal adaptability needs to encompass all of the factors that will either enhance or reduce adaptability (Gaughan and Cawdell-Smith, 2017). Furthermore, short-term and long-term strategies to enhance adaptation need to be considered.

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Broadly, adaptation is a nongenetic (short-term or phenotypic) and genetic (long-term or generational) response to a challenge (stressor). Nongenetic responses to a stressor may be short term such as reduced feed intake and increased respiration rates when exposed to high ambient temperature. However, short-term responses also have a genetic basis with some animals better able to cope than others when exposed to the same stressors. Many management strategies are short-term responses to acute challenges such as provision of shade and dietary manipulation. These reduce the challenge but don't lead to genetic change.

Productivity gains via targeted trait selection of ruminants are well documented. However, selection of animals for high levels of production has increased animal susceptibility to environmental challenges. For example, it is well accepted that high producing dairy cows are more susceptible to heat stress than low producing cows. Using lower production cows could reduce heat stress, lower milk output, and lower input costs. However, there would be a concentration of maintenance costs with a reduction in efficiency and increased greenhouse gas intensity. Optimum animal production is easiest, but not necessarily the most economical, to achieve under controlled environmental conditions, which is more often seen in nonruminant compared with ruminant production systems.

The challenges are many and do not always have a direct effect on animal performance. For example, chronic exposure to hot conditions may result in poorer pasture quantity and quality leading to poorer nutrition and nutritional outcomes which results in reproductive failure, poor growth, and increased disease risks. In this arena, animal adaptation is not necessarily paramount since it is more about getting nutrition correct and thus a whole farm approach is required (Thamo et al., 2017). The challenges are, to determine if there is a need for adaptation, a need for improved animal management (i.e., management and resource adaptation) or both.

Adaptation to What?

Enhancing animal adaptation will only work if other aspects of their environment/management are also adapted. For example, developing a heat tolerant bovine is of little value if there is insufficient feed and water to allow the genetic expression of the desired traits or if the productivity of these animals is extremely low. It is important that we understand that animal responses to a given set of stressors may change over time because the animal is adjusting to that stressor or challenge. While it is possible that acclimatization or adaptation may alleviate a stress response, the animal's performance (milk production, growth rate, fertility) may not return to the prestress levels. This is the conundrum or trade-off that livestock producers and animal breeders face. Adaptation is often at the expense of performance, and survivability is often better in "low" performance animals because their input needs (especially feed) and internal heat production are not as great (Gaughan and Cawdell-Smith, 2017). Stress tolerant animals tend to have lower productivity because they are adapted to the conditions. It was suggested by Colditz and Hine (2016) that there should be an increased focus on breeding and managing animals for improved resilience to applied stressors. They stated that husbandry practices that incorporate physical and social stressors plus interactions with humans could be used to characterize resilient phenotypes to a given set of challenges.

Key to our understanding of animal responses to a stressor(s), and indeed their ability to adapt, is to define the stressor(s), and define what we want the animals to adapt too. People often talk about the negative impacts of high ambient temperature on animal performance. However, animals are rarely exposed to a single stressor. For example, Sejian et al. (2013) discussed the effects of multiple stressors on sheep and concluded that the cumulative effects of excessive heat load, poor nutrition and the need to walk long distances to source feed and water compromised production and reproduction in Malpura ewes (an adapted native breed of semi-arid tropical regions in India). While a single stressor may be important, the cumulative effects of multiple stressors are significant, and some of these may be multiplicative rather than additive.

Adaptation Strategies

The strategies used to sustain ruminant production can be broadly classified as adaptation (e.g., developing tolerant breeds, improving water access, improved pasture species), mitigation/amelioration (e.g., nutritional interventions, manipulation of the rumen eco-system, provision of shade, housing, fans, and sprinklers; Table 1).

In a review of mitigation and adaptation needs of livestock, Zhang et al. (2017) stated that in general livestock producers have adapted to climate change by (1) shifting from cropping to grazing; (2) adopting mixed crop-livestock systems; and (3) decreasing stocking rates and/or herd sizes. However, they concluded by saying that the responses do not necessarily overcome all adverse effects that will be encountered.

There are no universal strategies. Some strategies may have global applicability, others regional, and others at a farm level. Of some concern is that there does not appear to have been any systematic global reviews on how the livestock sector is affected by and adapts to climate change (Escarcha et al., 2018).

Constraints to Adaptation

A recent review by Escarcha et al. (2018) listed a number of factors which are likely to constrain adaptation strategies. These include a lack of information at the systems level; lack of adequate research especially in Asia and South America; the fact that capacity building is highly dependent on government and other institutions; pastoral systems especially communal land tenure systems; limited access to natural, capital, and labor resources; poor market infrastructure and organization. Other areas constraining adaptation are a lack of trust in the science of climate change and the many unknowns regarding how climate change will impact on livestock systems.

Mechanisms of Adaptation

Morphological adaptation

Morphological adaptations include short and thin hair, light hair color, lightly pigmented skin, higher density of sweat glands, slender legs, and less subcutaneous fat. The coat is the

Table 1. Livestock adaptation strategies

Parameters for adaptation	Livestock adaptation strategies
Production adjustments	• Changes in quantity and timing of precipitation may shift timing of breeding, feed availability and water availability, and species mix
Genetics	• Identify existing breeds, especially "indigenous breeds" that are already adapted to climatic and nutritional stress • Identify the genes responsible for reducing stress • Functional genomics • Breed improvement through cross-breeding, and incorporation of "stress" tolerant genes
Science and technology	• Understanding of the impacts that environmental and nutritional stress has on animal performance and from this develop new breeds, improve animal health, and improve performance • Enhance soil and water management, develop drought and heat tolerant plants, improved grazing strategies, reduce runoff, and enhance soil fertility • Determine the climatic thresholds that lead to excessive heat load between breeds and species
Animal management systems	• Ensure that there is adequate shade and water to reduce heat stress • Ensure that housing is engineered to reduce the impact of high temperature/humidity • Ensure that housing is cost-effective • Reduce livestock numbers—match animal numbers to available resources • Change livestock species (goats instead of cattle) • Changing land use (land tenure) • Improved management of grazing lands (reduce over grazing and land degradation)
Capacity building	• Training in agro-ecological technologies and practices • Access to finance, energy, transport • Government policy

Adapted from Sejian et al. (2015), Gienapp et al. (2008), Thornton et al. (2009), Zhang et al. (2017), and Escarcha et al. (2018).

primary protective layer against the direct effects of solar radiation. Fanta (2017) reported that cows with light coat colors in tropical regions reflect solar radiation; thereby protecting the animal from the adverse effects of solar radiation. Whereas cattle with a dark coat color will absorb more solar radiation which increases their heat load. Cattle that are adapted to arid regions possess smooth, short and thin hair (slick hair gene) which enhances heat dissipation. Sweating allows animals to cope in hot climates. In cattle, thermo-tolerance is directly associated with the sweat gland density and sweating rate. Consequently, animals in hot regions maintain sweat glands with higher diameter, volume, perimeter, and density. In addition, cattle breeds in tropical regions tend to have a smaller body size as compared to temperate breeds (Sejian et al., 2018).

Sheep with light coat colors, which are sleek and shiny, reflect greater solar radiation than hair coats that are dark and dense or woolly. Furthermore, sheep with carpet wool protect themselves better from solar radiation by facilitating cutaneous heat dissipation (Sejian et al., 2018). Sheep with longer, thicker, and darker coats are subjected to greater stress and exhibit higher rectal temperature and sweating rates in tropical regions than white-haired sheep.

Goats are proficient desert-dwelling animals. Physiological characteristics of goats provides them an advantage over other ruminant species in harsh environmental conditions. Their small body size, fleece structure, and high digestive efficiency help them survive in harsh climatic conditions. Also, dwarf goats survive better in arid regions than other breeds, in part because their ears are short, erect and pointed forwards and their coat is a light color. Goats inhabiting arid zones possess long-hair, coarse-fiber fleeces to protect themselves from heat

during the day and cold at night. Furthermore, goats in temperate areas have a coat of long coarse fibers and a seasonal coat of short, fine fibers to protect against extreme cold.

Behavioral adaptation

Behavioral responses aid in the acclimatization process of animals when exposed to the high heat load. Behavioral responses studied in heat-stressed ruminants include shade seeking, reduced feed intake, increased water intake and drinking frequency, increased standing time, decreased lying time, and reduced defecation and urination frequency. Shade seeking is the most immediate behavioral response seen in heat-stressed animals. Typically, dairy cattle use shade on clear days once air temperature exceeds 21 °C, and the duration of shade use increases as air temperature and solar radiation increase, with cows often spending over 10 h per day under shade. Shade usage reduces grazing time and subsequently reduced milk production or reduced growth. Sheep, although typically more resilient, will also seek shade during exposure to elevated temperatures.

Reduced feed intake is an adaptive mechanism which reduces metabolic heat production in animals during summer. Numerous studies have reported reduced feed intake in cattle, sheep, and goats during exposure to heat (Valente et al., 2015; Aleena et al., 2018). Furthermore, Curtis et al. (2017) opined that behavioral studies showed variation in grazing patterns of extensively managed cattle under hot conditions with lower and higher grazing time during the day and night, respectively. Increased water consumption and drinking frequency occur in various ruminant livestock during hot conditions (Valente et al., 2015; Aleena et al., 2018). Brscic et al. (2007) established that heat-stressed cattle had a reduction in urination frequency while Chedid et al. (2014) reported that desert sheep compensate for the higher water loss by concentrating their urine during extreme heat load. Standing and lying time is also affected by high heat load. Heat-stressed sheep and cattle tend to spend more time standing to reorient themselves to avoid direct solar radiation and ground radiation.

Physiological adaptation

Physiological adaptability is one of the primary response mechanisms that aids animal survival during exposure to high heat load. Exposure of animals to heat load induces an increase in the dissipation of excess body heat to the environment to reduce the heat load in their body. Further, dissipation of excess body heat is brought on by the physiological responses including increased respiration rate, rectal temperature, pulse rate, skin temperature, and sweating rate. Physiological responses show distinct diurnal variations during the daytime while the values remain stable during the night (da Silva et al., 2017). Reducing body heat at night helps the animals cope with higher temperature during the daytime. Respiration rate and rectal temperature are ideal indicators for quantifying heat stress in several ruminant species (Chauhan et al., 2014).

Blood biochemical adaptation

Heat stress results in altered blood biochemical parameters. Heat stress induces an increase in hemoglobin and packed cell volume in cattle, and these changes are considered to be a gradual development of adaptive characteristics in cattle (Mazzullo et al., 2014). Furthermore, there are several hormones which are involved in controlling the mechanism of homeothermy in ruminant animals. In an effort to adapt with higher ambient temperatures, animals reduce the secretion of thyroid hormones to control metabolic activities and thus the production of body heat. Additionally, cortisol is the primary biochemical marker for heat stress in ruminant livestock. Substantial increases in levels of cortisol during heat stress indicates the stress level of ruminants (Sivakumar et al., 2010; Sejian et al., 2013). Superoxide dismutase and glutathione peroxidase are indicators of oxidative stress in sheep and cattle, particularly during exposure to excessive heat load. An increase in the concentration of these antioxidants was reported in sheep (Chandra and Aggarwal, 2009; Chaudhary et al., 2015) and dairy cattle (Bernabucci et al., 2002).

Metabolic adaptation

When exposed to high heat load, the secretion of leptin and adiponectin are up-regulated, where leptin stimulates the hypothalamic axis resulting in a reduction in feed intake, while adiponectin changes the feeding behavior by peripheral and central mechanisms. Verma et al. (2000) attributed this decreased feed intake to the direct effect of increased temperature on the satiety center of the hypothalamus. Changes in the concentration of thyroid hormones in blood reflect the metabolic and nutrient status of the animal. The difference in the bioactivity of these hormones helps to maintain metabolic balance under stressful conditions, particularly in grazing animals since they are vulnerable to fluctuating environmental changes (Todini et al., 2007). It has been established in sheep that the decreased function of the thyroid gland during exposure to high heat load is a metabolic adaptation to reduce metabolic heat production.

Increased ambient temperature can also directly affect the hypothalamic–pituitary axis and reduce thyroid stimulating hormone secretion. Decreased thyroid stimulating hormone production reduces thyroid gland function and circulating T3 and T4 hormones in an effort to reduce metabolic heat production. However, Chauhan et al. (2014) saw no change in cortisol, T3 or T4 in sheep exposed to excessive heat load.

Metabolic activities are also controlled by several enzymes. Plasma alkaline phosphatase and alanine aminotransferase concentrations generally increase in heat-stressed dairy cows. Serum alanine aminotransferase concentrations also increase in response to heat stress in sheep. The change in alanine aminotransferase and alkaline phosphatase during heat stress are indicators of poor liver function. Thus, both may be good markers in susceptible animals. Furthermore, nonesterified fatty acid also plays a crucial role in determining the energy status of livestock. Nonesterified fatty acids have a predominant role in maintaining metabolic activities through its timely mobilization to liver and peripheral tissues as a source of energy during periods of heat stress. Heat stress results in a considerable decline in nonesterified fatty acid concentrations in lactating cattle (Baumgard and Rhoads, 2013).

Biological markers. Genetic differences in thermo-tolerance at the physiological and cellular levels in ruminant livestock have been well documented. Heat tolerance is a quantitative trait. One of the dominant genes identified to impart thermo-tolerance is the slick hair gene, which controls the length of hair in cattle. Apart from this, other genes such as ATPase Na+/K+ transporting subunit alpha 1 and ATPase Na+/K+ transporting subunit beta 2, thyroid hormone receptor, fibroblast growth factor, and heat shock proteins were found to be associated with heat tolerance in ruminants (Collier et al., 2012; Aleena et al., 2018). The ATPase Na+/K+ transporting subunit alpha 1 gene has also been associated with various heat tolerance variables including respiration rate and rectal temperature in both Tharparkar and Vrindavani cattle breeds suggesting that it may be a good biological marker for thermo-tolerance. Recently, researchers have established a rapid induction of heat shock protein-70 mRNA expression in goats during heat stress exposure confirming its role in heat tolerance (Aleena et al., 2018). In addition, polymorphisms in heat shock protein-90AA1 were also found to be associated with heat tolerance in Frieswal cattle (Deb et al., 2013) and sheep breeds (Marcos-Carcavilla et al., 2010). Increased expression of immune response genes such as a toll-like receptor, toll-like receptor 2/4 and interleukins 2/6 were also documented in heat stressed Tharparkar cattle. It is likely that these genes are associated with thermo-tolerance (Bharati et al., 2017). In a recent review, Sejian et al. (2018) identified respiration rate, rectal temperature, cortisol, plasma heat shock proteins-70, toll-like receptor-2, toll-like receptor-1, toll-like receptor-4, toll-like receptor-5, and heat shock proteins-70 genes to be useful biological markers for quantifying the impact of multiple stressors in both sheep and goats.

Knowledge of the impact of heat stress on the various adaptive responses provides clear insight into future ruminant livestock production. The various biological markers identified for the heat stress condition may also help researchers develop climate resilient breeds based on both phenotypic and genotypic markers involving morphological, behavioral, physiological, cellular, and molecular processes. In addition, combining the various identified biomarkers may help to look beyond thermo-tolerance in livestock and may go a long way to identify a breed or breeds with superior thermo-tolerance for optimum productivity. Therefore, with the advancement in assessing the various mechanisms associated with thermo-tolerance, it is possible to secure and sustain future ruminant livestock production by promoting welfare and favoring survival in a specific environment.

Conclusions

Livestock are important contributors to total food production. Animal products are high-quality food, and they are an important source of income for many farmers in developing countries. Therefore, sustaining livestock production in a changing climate is one of the top priorities in the agriculture sector. Reducing the adverse impact of climate change on livestock requires multidisciplinary approaches including the integration of animal breeding, nutrition, housing, and health. It is essential to understand and analyze livestock responses to the environment, to design modifications of nutritional and environmental management strategies and thereby improve animal comfort and performance. However, in developing a strategy for adapting to climate change, one key challenge is dealing with uncertainty. Livestock producers should have key roles in determining the appropriate adaptation and mitigation strategies to use to sustain livestock production in a changing climate. The integration of new technologies into the research and technology transfer systems potentially offers many opportunities for further development of strategies to adapt to climate change.

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Terry L. Mader is Professor Emeritus at the University of Nebraska, Department of Animal Science. Dr Mader earned his BS from Kansas State University and his MS and PhD in Animal Nutrition from Oklahoma State University. Dr Mader's current activities include involvement in national and international projects studying and mitigating environmental effects on animal productivity. He is past-Chairman of the FASS Beef Cattle subcommittee on the Guide for Care of Agricultural Animals and the Professional Animal Auditors Certification Organization, affiliated with American Registry of Professional Animal Scientists. Dr Mader is a previous recipient of the American Society of Animal Science Animal Management Award and an honorary professor of Animal Production at the University of Queensland in Australia. He is author or co-author of over 400 scientific publications. Dr Mader is currently Head of Mader Consulting, LLC, a business entity devoted to the development of management strategies and models to minimize stress and effects of climate variability in livestock.

Frank Dunshea is a Professor with a more than 30-year research career in the area of growth physiology and nutrition and the use of domestic animals in nutritional and biomedical research. He has published more than 750 journal, conference, book, patents, or technical articles. His research has had a high scientific impact, with many of the results being rapidly adopted by industry. Professor Dunshea is a respected research leader in global livestock industries and is committed to ensuring that livestock industries operate in a responsible and sustainable manner. Much of his work has focused on improving efficiency through reducing inputs and outputs while maintaining product quality and consumer health including an emphasis on mitigation against heat stress. In addition to many awards, he is a Fellow of the Australian Nutrition Society, the Australasian Pig Science Association, and the Australian Society of Animal Production as well as a former Chair of the Australian Academy of Science Committee for Nutrition.

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Feature Article

Heat stress adaptations in pigs

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Implications

- Heat stress is a global issue constraining animal agriculture productivity, negatively affects welfare, and reduces production efficiency in many countries.
- The effects of heat stress on pig production will intensify, if climate change continues as predicted.
- To date, modifying the environment is the most effective way to mitigate the effects of heat stress.
- Identifying additional strategies (nutritional and genetics) to maximize pork production during the warm summer months is necessary to satiate a growing demand for high quality meat for human consumption.

Key words: adaptation, heat stress, management, swine

Introduction

Heat stress is a major environmental issue negatively affecting animal welfare and production efficiency in almost every livestock sector (Baumgard and Rhoads, 2013). When animals are exposed to environmental conditions that exceed their thermoneutral zone, production efficiency is compromised because the hierarchy of nutrient utilization is reprioritized to maintain euthermia, and consequently productivity is deemphasized. Heat stress is not an issue limited to tropical regions, as temperate countries are also affected during warm summer months (Renaudeau et al., 2012a). In fact, estimated annual losses due to heat stress in the U.S. livestock industry alone is US$1.5 billion for dairy and nearly US$1 billion for swine (Pollmann, 2010; Key and Sneeringer, 2014). Furthermore, increased genetic selection for production traits (i.e., lean tissue accretion, milk yield, and fecundity) leads to reduced heat stress tolerance as these phenotypes are associated with increased metabolic heat production (Renaudeau et al., 2012a; Baumgard and Rhoads, 2013).

In the swine industry, economic losses associated with heat stress are mainly explained by reduced and inconsistent growth, decreased feed efficiency, decreased carcass quality (increased lipid deposition and decreased protein accretion), poor sow performance, increased mortality (especially in sows and market hogs) and morbidity, and decreased facility efficiency (Baumgard and Rhoads, 2013; Ross et al., 2015). Reduced reproductive performance is characterized by anestrus, increased wean-to-estrus interval, decreased farrowing rate, and reduced litter size (Ross et al., 2015). Similarly, poor semen production and quality occur in boars exposed to heat stress. Thus, heat stress compromises almost every economically important phenotype within the industry.

Although the aforementioned postnatal effects of heat stress are easily recognized and well-defined, the effects of in utero heat stress experienced by the developing piglet on future postnatal production traits are more inconspicuous. Specifically, piglets derived from heat-stressed dams have increased body temperature and accumulate adipose tissue more efficiently during later growth stages at the expense of lean tissue (Johnson et al., 2015; Ross et al., 2017). Both increased body temperature and altered body composition have profound implications on maintenance costs, feed efficiency, ration formulation, and facility efficiency. However, these inefficient phenotypes would be expressed during the following year's winter and spring and would thus be less remarkable. The prenatal effects of heat stress on future production phenotypes (which are currently not considered in the economic estimates) may ultimately be a larger constraint to efficient pig production than the more distinguishable effects of postnatal heat stress.

General Context of the Evolution of the Global Pork Production

Globally, pork is one of the most consumed farm animals (Figure 1). China has about half of the pork production (49%), European countries are the second largest in pig production (25%), and North American countries are third with 11% (Figure 2). When considering growth rates between 1990 and 2016, emerging countries (e.g., South America and South Eastern Asia) are expected to contribute more significantly to global pork production with lower growth expected in Europe and North America. Incidentally, many of the aforementioned regions of expected growth in pig production are characterized by long periods of warm and humid conditions. Coupled with a rapidly expanding human population is an expected decrease in poverty rates. In this context, worldwide appetite for pork is expected to increase by 50% by 2050, especially in emerging

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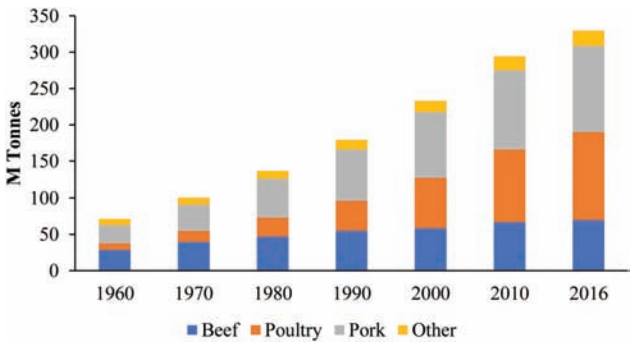


Figure 1. Evolution of the world market demand for meat production between 1960 and 2016 (FAO Statistics).

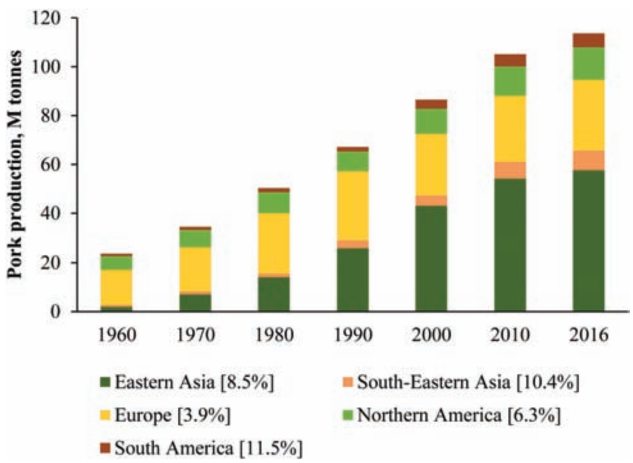


Figure 2. Evolution of pig meat production per country across 60 yr (FAO Statistics). Data enclosed in square brackets are the yearly variation in pork production from 1990 to 2016.

tropical and subtropical countries. In most cases, the expansion in pig production will be achieved through intensification based on modern management practices and on animals of high genetic merit.

However, the environment where pork is actually produced is often markedly different from the conditions where the genetic selection occurred. Consequently, climate change combined with the migration of pig production and a suboptimal genetics by environment interaction creates a significant barrier of sustainably meeting the global requirement for animal protein.

Biological Adaptation/Acclimation

Thermoregulation

Animals lose heat in the form of sensible and latent (evaporative) heat. Conduction, convection, and radiation are primary mechanisms sensible heat loss occurs, and each requires a temperature gradient between the animal and its environment (Collier and Gebremedhin, 2015). Therefore, as ambient temperature increases, animals redistribute blood towards the skin in an attempt to increase radiant heat loss. With a further increase in ambient temperature (the temperature gradient between the environment and animal becomes smaller or even negative), the transfer of heat by conductive, convective, and radiative modes decreases. In fact, when ambient temperature increases above the upper critical temperature, evaporation is the only route of heat loss. Swine have few functional sweat glands and their thermoregulatory ability is further complicated by a thick subcutaneous adipose tissue layer, which impedes sensible heat loss; thus, pigs depend more on the respiratory route (i.e., panting) for heat dissipation (Collier and Gebremedhin, 2015). If the efforts of increasing heat loss to maintain euthermia are inadequate, the pig will initiate a variety of strategies to minimize heat production (behavior, etc., discussed below).

Feed Intake and Growth Performance

Normally, adjusting voluntary feed intake is one of the main adaptations employed to modify metabolic heat production in response to ambient temperature changes. Therefore, when ambient temperature increases, euthermia is maintained mainly by increasing heat loss and reducing heat production (Collin et al., 2001). Strategies to reduce heat production include decreasing feed intake and its associated thermic effect of feeding (Quiniou et al., 2000), along with decreased physical activity and reducing basal metabolic rate (Collin et al., 2001). Reduced feed intake is a highly conserved response to heat stress across species (Baumgard and Rhoads, 2013), and in pigs it can be represented as a curvilinear decrease with increasing ambient temperature, but varies depending on genotype, diet composition, body weight, and ambient temperature (Renaudeau et al., 2011).

Average daily gain during heat stress is usually reduced, and this is partly a consequence of decreased nutrient intake. Similar to feed intake, average daily gain has a curvilinear response during a thermal load and is affected by the animal's body weight with heavier pigs more susceptible to heat stress than lighter ones (Renaudeau et al., 2011). As reviewed by Renaudeau et al. (2012b), the effect of heat stress on feed efficiency depends on both the temperature level and pig body weight. For a mild heat stress, feed efficiency generally increases because of the effect of feed restriction on the composition of body weight gain (more lean/less fat). Reduced feed efficiency is reported in finishing pigs kept at a temperature higher than 30 °C. This decrease in feed efficiency is related to a reduced proportion of energy intake available for tissue growth, which is mainly explained by a strong reduction in feed intake. However, regardless of the nuances within the feed efficiency equation, there is no question that heat stress reduces facility and operational efficiency (amount of carcass weight produced per barn per year) as it markedly decreases the time it takes to reach market weight.

Interestingly, variations in growth performance during heat stress may also depend on the severity of the heat load and this is especially true when compared with pair-fed thermal neutral controls (Figure 3; Pearce et al., 2013; Sanz Fernandez et al., 2015). During mild heat stress (determined by small increases in body temperature variables and only mild reductions in feed intake), pigs grow slower than the pair-fed controls. However,

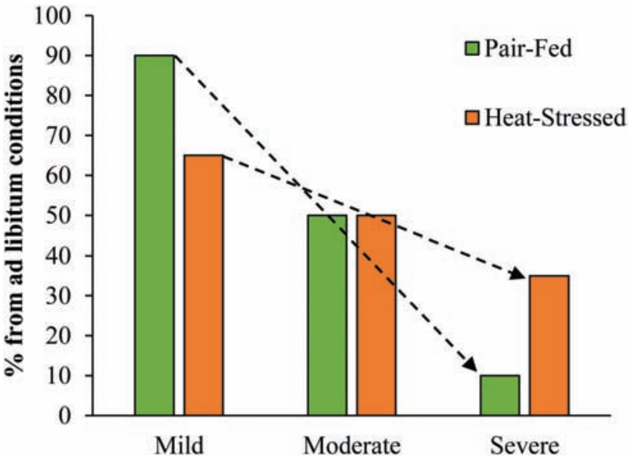


Figure 3. The effects of increasing severity of heat stress on growth rates when compared with ad libitum feeding in thermal neutral conditions.

as the severity of heat stress intensifies (determined by large increases in body temperature variables and severe reductions in feed intake), the heat stress pigs perform better (from a growth perspective) than pair-fed thermal neutral controls. This is energetically perplexing but is likely due to the fact that severe heat stress actually decreases maintenance costs rather than increasing it as reported previously (reviewed in Baumgard and Rhoads (2013) and Johnson et al. (2015)).

What Will Be the Main Impact of Future Climate Change on the Swine Industry?

Despite uncertainties in climate variability, the IPCC Fifth Assessment Report Climate (2009) concluded that the increase in global average surface temperature during the 21st century will likely be almost 5 °C, depending on the greenhouse gas emission scenario. Additionally, it reports that it is "virtually certain" that heat waves will occur more often and last longer, and that extreme precipitation events will become more intense and frequent. The deleterious impact this will have on the pig industry is obvious, but given the large uncertainty in the evolution of greenhouse gas emissions (within the global and local socioeconomic context), attempts to accurately evaluate future economic consequences for pork production in response to the global climate change are difficult. Despite the complexity of the assessment, this information is a prerequisite for developing adaptation strategies and implementing decisions.

Regarding the effect of global warming on crop production, most models predict a slight to moderate negative effect on simulated yield, even when beneficial effects of CO_2, farm-level adaptations, and future technological yield improvements are accounted for (Parry et al., 2004). However, these simulations do not account for uncertainties related to water availability for irrigation and to the potential impacts of pests, weeds, and others stressors (Tubiello et al., 2007). An often overlooked consequence (likely because it is not well-understood) of heat stress and future climate change is the negative effects it may have on the plants eventually consumed by farm animals (Baumgard et al., 2012). For example, climate variability will likely increase instances of mycotoxin production, especially in temperate climate regions (Magan et al., 2011) and pigs have limited ability to detoxify mycotoxins (Wu et al., 2010). Additionally, the crop's nutrient composition will likely change as protein content is expected to decrease and digestibility may be negatively affected (Hristov et al., 2018). Regardless, despite the fact that the effects of climate change on composition and digestibility of cereals and protein sources remain relatively vague, the potential for altered nutrient feeding value to negatively affect pig production is real and needs to be incorporated into future predictions.

Intervention Strategies

There is already a dire need to develop effective and sustainable management approaches to mitigate the negative effects of heat stress and this is even more important within the context of climate change. Undoubtedly, the primary priority is to modify the animal's microenvironment and these heat stress abatement strategies are presented below. However, the input cost for optimal cooling technology is often too expensive, and this is particularly true for small stakeholders and farmers in developing countries. Genetic selection for thermal tolerance is one potential strategy to mitigate the effects of heat stress, but this is a long-term solution, and typically accompanied by reduced productivity during thermal–neutral conditions. Identifying flexible management approaches to immediately decrease heat stress susceptibility without negatively influencing traditional production traits would be of great value to global animal agriculture. Dietary supplementation and modifications (discussed below) are easily adjustable tactics that could be utilized by a variety of animal industries and are amenable to diverse production systems.

Heat Stress Abatement Strategies: Environment Modification

There are multiple engineering solutions and management strategies that can be used to mitigate heat stress, with physical environment modification the most effective. Foremost, facility design, construction, and operation are the initial mechanisms for 1) limiting amplification of ambient conditions and 2) minimizing energy required to remove heat from the system. A facility engineered with factors such as shape and orientation, thermal characteristics of construction materials, and ventilation system in careful consideration creates the foundation in which productivity can be minimally disrupted during heat stress.

Characterizing the Thermal Environment

As mentioned above, the thermal environment describes the parameters that influence thermal (heat) exchange between an animal and its surroundings. As previously explained, sensible heat loss modes (conduction, convection, and radiation) are driven by a temperature gradient and latent heat loss modes (evaporation) by a water vapor pressure gradient between an animal's outer surface (skin or pelage) and its surroundings. Animal characteristics (i.e., configuration, surface area, and surface temperature) affect all sensible modes (surface emissivity only affects radiation). Environmental characteristics each uniquely affect the different heat loss modes, such as surrounding surface temperatures (conduction and radiation), dry-bulb temperature (convection), air velocity (convection and evaporation), vapor pressure (evaporation), emissivity and orientation of surrounding objects (radiation), and lastly, heat capacity and thermal resistance of contact object (conduction). Therefore, these are the environmental parameters that can be physically modified to reduce heat stress (Figure 4).

The need to predict and support informed management decisions related to animal performance, health, and well-being has resulted in the development of thermal indices or equivalent (effective) temperatures that represent the effects produced by the heat exchange process. Although these indices substantially simplify complex physical and biological interactions, they serve as useful tools for guiding thermal environment management. For swine, the thermoneutral zone range changes predominately as a function of body mass. This is attributed to the increasing metabolic heat production and the decreasing surface area to mass ratio as a pig grows, albeit body mass is rarely ever used as an input to a thermal index, it is required to accurately assess the thermal environment. Consequently, the exact environmental conditions inducing heat stress in pigs remain ill-defined and this limits the effectiveness of heat stress abatement management.

Environmental Modification

Solar Radiation

For outdoor animals, reducing the solar radiation load by providing shade is presumably a cost-effective and simple method. Trees or artificial barriers (such as galvanized sheeting, shade cloth, and plastic snow fence) can minimize exposure to direct solar radiation, reduce the surrounding surface temperatures (radiated/reflected heat back to the animal), and does not modify the local thermal environment. Design considerations for shade structures include orientation, pitch, height, and material (da Silva and Maia, 2012). Conversely, for housed animals, although they are rarely exposed to direct solar radiation, it can substantially heat a facility's roof, attics, and ceilings leading to facility heat accumulation inducing a higher infrared radiative load (long-wave radiation; Hoff, 2013). Thus, ceiling and attic insulation are effective methods at reducing the indoor surface temperature and heat accumulation.

Air Conditioning

Air temperature can be reduced using a direct expansion air conditioning unit, which consists of a mechanical system and refrigerant circulation. However, the capital, operational, and material longevity typically make it economically unviable for swine applications.

Evaporative Pads

When water changes phase from liquid to vapor (i.e., evaporation), energy is needed (about 2425.5 kJ kg_{H2O}^{-1} at 32 °C). As outside air enters an evaporative pad, energy is removed from both the wet pad and the air as the water evaporates, thereby decreasing air temperature. Hence, the air temperature entering the facility is lower (since heat was removed for evaporation) and the relative humidity as well as the water vapor content is greater. Application of evaporative pads is most commonly used in breeding herd facilities (sows/boars) where cooling demand is greater and the need for dry surroundings are desired.

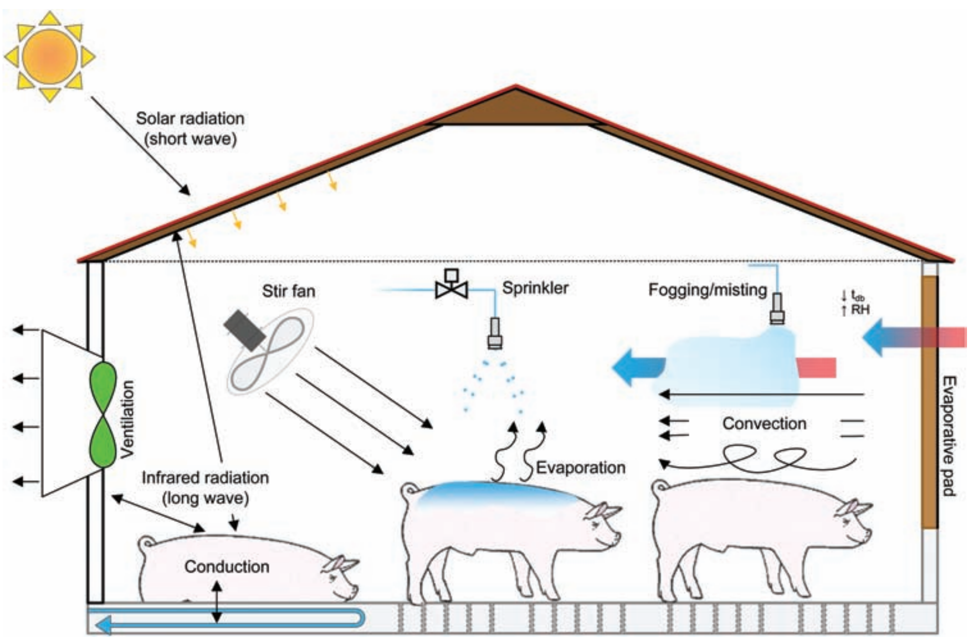


Figure 4. Thermal (heat) exchange between a pig and its surroundings with prediction of different cooling strategies as they relate to heat exchange.

Fogging/Misting

Fogging (pressure > 5 MPa) and misting systems (pressure ≤ 5 MPa) reduce air temperature via water evaporation. The portion of airborne-atomized water that evaporates increases with decreasing droplet sizes (Haeussermann et al., 2007). Fogging systems create very fine droplets usually achieved by high-pressure, atomizing nozzles placed at fresh air inlets and wetting of surrounding surfaces is generally avoided, since evaporation can occur in relatively high humidity. Conversely, misting systems generate larger droplets (low pressure) that do not fully evaporate while airborne and can wet surrounding surfaces and animals. With all cooling systems utilizing water evaporation, the evaporation rate, and subsequently, heat removal, is limited by the amount of air moisture.

Direct Cooling

As opposed to physical modifying the environment to provide a cooler effective temperature, direct cooling involves the increase in heat loss from the body surface. Different strategies are discussed below.

Elevated Airspeed

Air movement over the animal affects both convective and evaporative heat loss. Convective heat loss increases at approximately the square root of air velocity; hence, as airspeed increases, the convective heat loss benefit diminishes. Furthermore, a temperature gradient between the animal's surface temperature and the air temperature must exist for heat loss to occur. Typical swine skin temperature fluctuates between 32 and 36 °C. Thus, if ambient temperature approaches skin temperature, the effectiveness of elevated airspeed/"wind" (without utilizing evaporative cooling) is minimized. Elevated airspeeds can be accomplished by increasing airflow per unit of cross-sectional area (principle behind tunnel ventilation), stir (mixing) fans, or the wind in naturally ventilated facilities.

Wetted Skin

Adding water to the pig's skin can increase heat loss and if combined with elevated airspeeds becomes a powerful tool for heat stress alleviation. Heat directly from the animal (and to some extent the surrounding air) is transferred to the evaporating water (the phase change requires energy). The transfer of thermal energy from the pig into the evaporating water thereby decreases the pig's body temperature. Large water droplets needed to wet the skin can be distributed by low-pressure sprinklers for covering larger areas or "drippers" for localized cooling (i.e., sows in a snake). Coupling intermittent water application with elevated airspeed can markedly improve the efficiency of both routes of heat loss.

Floor (Conductive) Cooling

Pigs can lose sensible heat to a solid material of a lower temperature through contact. This is predominately achieved by circulating cool water through the floor the pigs lie on. Lactating sows spend a majority of their day lying, and this behavior allows for the effectiveness of chilled floor plates. For finishing pigs, concrete slats have been casted with piping to allow for water circulation. Economic viability is limited as capital and operational costs can be substantial, in conjunction with the technical feasibility of establishing a chilled water source and designing a pipe distribution network.

Monitoring

There are several technologies that exist for monitoring the thermal environment and animal physiological responses to heat stress. Effective and real-time monitoring is necessary to make appropriate investment decisions regarding heat stress abatement.

Environment

Air temperature is often the only parameter used to manage and describe the thermal environment and this results in multiple sensing options. The main characteristic of a good sensor for swine housing is 1) ability to quickly respond to changing conditions (i.e., low thermal mass) and 2) minimal radiative load (shielded). Long-wave infrared radiation can increase the temperature of the sensing element and cause the false indication of a high air temperature; however, this also most likely indicates a high radiative load and the need for additional cooling. Accurately measuring relative humidity was once challenging, given the dust and gaseous concentrations found in swine housing, but filters and newer sensing technologies have reduced sensor cost and extended longevity. Airspeed is virtually unmeasured due to sensor cost and ability to monitor from near still air conditions (~0.12 m s^{-1}) to elevated airspeed for convective cooling (>2 m s^{-1}). Lastly, long-wave infrared radiation is often neglected due to a lack of practical data interpretations. Nevertheless, the ISO 7726 (2001) states that a 15.24-cm diameter, copper sphere painted flat black with an air temperature sensor at the center is the standard.

Animal

The predominate physiological responses measured as an indicator of heat stress are respiration rate, skin temperature, rectal temperature, tympanic temperature, and vaginal temperature. Accurately measuring core-body temperature would be an ideal metric but this is accompanied with obvious hurdles. Good proxies for core-body temperature are rectal, vaginal, and tympanic membrane temperature, but obtaining these requires restraint and proper training and each has potential negative side effects. Respiration can be simply counted via human observation as the chest cavity expands and contracts, while automatic monitoring respiration rate in swine has been achieved. Skin temperature reflects the balance between metabolic heat production and the heat loss to the surroundings. With regards to skin temperature, both sides of the thermal balance must be known; that is, heat produced from the animal (core body temperature, tissue resistance, peripheral blood flow, respiration, passive skin diffusion, and pelage temperature) and energy removed from the animal (sensible and latent modes of heat transfer requiring surface area, shape and orientation, and all the environmental measurements). Thus, although frequently measured during environmental physiology experiments, skin temperature has little utility in determining the severity of heat stress.

Nutritional Considerations for Heat Stress

Nutritional interventions represent a practical, adaptable, and cost-effective opportunity to ameliorate the negative effects of heat stress and improve animal productivity. Typical dietary management practices include formulating low thermic effect of feeding diets and this is primarily accomplished by increasing dietary fat and reducing the amount of crude protein or crude fiber. Digesting, absorbing, and assimilating dietary fat generate the least amount of heat compared with other nutrients. Fermenting fiber in the large intestine generates heat and metabolizing excess dietary protein is associated with increased heat production, so minimizing fermentative diets and accurately predicting protein and amino acid requirements during the warm summer months should help pigs cope with a heat strain (Patience et al., 2015). It should be emphasized that these dietary recommendations are in large part theoretical and evidence supporting them are not as abundant and overwhelming as expected. In fact, Rauw et al. (2017) recently reported that performance in growing pigs exposed to repeated episodes of heat stress was not affected by a high-fiber diet. Consequently, the applied nutrition field needs systematic research that challenges long-held dogmas regarding diet formulation during the warm summer months.

Other dietary strategies involve supplementing bio-active compounds that have utility beyond their requirement (Rhoads et al., 2013). Many of the negative consequences that heat stress has on animal health and productivity are mediated by reduced intestinal barrier integrity (Baumgard et al., 2012; Baumgard and Rhoads, 2013). As already mentioned, during heat stress there is a redistribution of blood to the periphery in an attempt to increase heat loss. Consequently, the gastrointestinal tract vasoconstricts in an effort to support the altered blood distribution and the reduced splanchnic blood and nutrient flow creates intestinal barrier dysfunction. Intestinal infiltrating antigens stimulate a local immune reaction and, if severe enough, cause systemic endotoxemia associated with inflammation and an acute phase protein response. Consequently, heat stress is in large part an immune response caused by "leaky gut." Thus, dietary strategies to prevent or minimize intestinal hyper-permeability are of particular interest and include antioxidants (selenium, vitamin E, vitamin C, etc.), specific amino acids (i.e., glutamine, betaine), and minerals (i.e., zinc). Additionally, functional molecules that have immunomodulatory effects could potentially ameliorate production loses during heat stress and these include chromium and vitamin C.

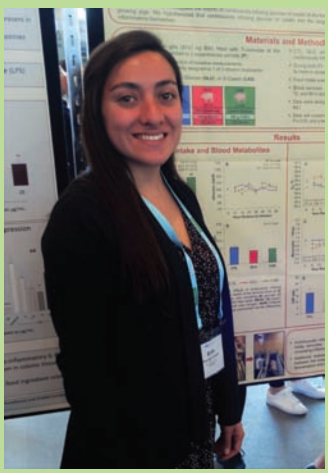
Genetic Opportunities

As stated above, heat stress susceptibility will worsen if genetic selection continues to emphasize traditional production traits, as these are associated with increased heat production. Fortunately, heat susceptibility appears to be a heritable trait in finishing pigs, and therefore, genetics may offer a viable strategy to improve production during the warm summer months. The biological and phenotypic responses to heat stress represent an extremely complex trait for which genetic information is insufficient. In recent work, many significant genomic regions in relation with heat tolerance were identified in pigs (Riquet et al., 2017). This new genomic information could be used in the future to identify pigs capable of maintaining high levels of productivity during heat stress. However, there remains a considerable knowledge gap and a critical need to improve our understanding of the genetic contributions to the variation in response to heat stress.

Summary

In summary, heat stress compromises a variety of production parameters in the swine industry including growth, carcass composition, and reproduction. Evidence suggests that maternal exposure to heat stress has long-lasting effects on postnatal offspring performance. The combination of climate change forecasts increased pork production in tropical and subtropical regions of the globe and improved genetic capacity for lean tissue accretion and fecundity, all point to increasingly negative impacts of heat stress on pork production efficiency and quality in the future. Physically modifying the environment is currently the primary abatement strategy that should be utilized to mitigate the negative effects of heat stress, but other approaches include dietary modifications and genetic improvement.

About the Author



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Dr. Jason W. Ross is the Lloyd L. Anderson Endowed Professor in Physiology in the Department of Animal Science at Iowa State University and Director of the Iowa Pork Industry Center. His research program utilizes basic and applied research approaches to test hypotheses from which the results will help enable livestock producers and associated industries improve swine production efficiency. His research efforts include genetic modification of pigs to improve understanding the genetic control of phenotypes associated with production efficiency and to improve the use of pigs as biomedical models. Dr. Ross earned his BS at Iowa State University, his MS and PhD at Oklahoma State University and was a postdoctoral research fellow at the University of Missouri.

Dr. Lance Baumgard is the Jacobson Professor in the Department of Animal Science at Iowa State University. His research efforts are primarily in Environmental and Nutritional Physiology. His scientific focus is on learning how heat stress reduces farm animal activity and to develop nutritional/management strategies to ameliorate heat stress. **Corresponding author:** baumgard@iastate.edu

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Feature Article

Selecting for heat tolerance

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Implications

- Identification of heat tolerant animals is challenging due to the complexity of heat stress response and the antagonism between heat tolerance and productivity. Advances are needed to: 1) find fine phenotypes to identify heat tolerant animals on farm; 2) develop methods to combine the knowledge from all "-omics" technologies.
- Breeding strategies to improve heat tolerance will depend on the production system. Systems that can provide enough resources to ensure high productivity will benefit more from including heat tolerance in the breeding programs of specialised breeds. In contrast, production systems with scarce resources will benefit more from crossing with local stock.

Key words: heat tolerance, breeding tools

How Do We Measure the Heat Tolerance of Animals?

It is not obvious how to define a heat-tolerant animal. In principle, a heat-tolerant animal is one that maintains homeothermy under high environmental heat loads. However, from a livestock breeding point of view, maintaining productive and reproductive levels under hot conditions may be the target. Maintaining homeothermy under hot conditions depends on the animal's ability to balance thermogenesis and heat dissipation. Several measures have been proposed as criteria to identify heat tolerant animals; these include body temperature, respiration rate, heart rate, and sweating rate. Animal performance under heat stress is a way of measuring the overall ability of the animal to cope with heat. Hair and coat characteristics including hair shedding rate and body surface to mass ratio are related to the animal's ability to dissipate internal heat. These measures have also been proposed as heat tolerant traits (Gray et al., 2011). Several biomarkers such as blood parameters (Van Goor et al., 2016) or diverse molecules associated with the heat stress response have also been proposed as indicators of heat stress in livestock (Min et al., 2017).

From the perspective of the implementation of a selection program for heat tolerance, measures that can be collected easily under farm conditions at a low cost are needed. Most of the efforts to implement genetic evaluations for heat tolerance have used performance recording under heat stress, following the original developments of Ravagnolo et al. (2000). Information of weather conditions (temperature and humidity most often combined in the temperature humidity index proposed by NRC, 1971) on the day or previous days of performance recording is merged with performance records to quantify the reaction of animals to heat loads in terms of productivity. This approach has the advantage of low cost, since performance recording is already available in livestock breeding schemes, but it also has some drawbacks. The first limitation is due to the ability to produce accurate measures of heat tolerance from existing recording schemes, which are not designed to capture the heat stress response. An example of this is shown in Freitas et al. (2006), where the heat stress response was largely underestimated when comparing the monthly recording (normally used in milk recording) to a weekly recording. Another limitation is related to the antagonism between productive level and heat tolerance. Thus, selecting animals with smaller slopes of decay in performance at high temperatures may decrease the productive level in the population, as it will be later illustrated.

Physiological traits such as body temperature or respiration rate are considered as gold standard measures for heat tolerance, but their use in large-scale selection programs is still limited because it is expensive to collect these measurements. Advances in the development of devices that can produce measures automatically at a low cost might change the possibility of using these types of measures in breeding programs in more intensive production systems (Koltes et al., 2018).

Quantification of levels of heat stress biomarkers could be achieved at a low cost in dairy populations through the use of mid-infrared spectroscopy that are routinely obtained to determine the main components of milk. The milk spectra could be calibrated to quantify the level of metabolites or other substances identified as biomarkers of heat stress, providing a

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potentially inexpensive tool to identify heat tolerant animals. However, the complexity of the heat stress response makes the selection of a reduced number of key biomarkers a difficult task. Recently, Hammami et al. (2015) explored the use of mid-infrared spectroscopy to assess profiles of milk fatty acids as possible biomarkers for heat stress in dairy cattle.

The Genetic Component of Heat Tolerance

As described above, genetic selection might be a cost-effective tool to improve thermotolerance of animals. However, for genetic selection to be effective, it is necessary to have a deep knowledge about the genetic basis of the animal's response to heat stress. Many studies have used different genetic tools to study the genetic basis of heat stress including, classic quantitative genetics as well as the more recent "omics" technologies. All of these technologies have the main goal of understanding what makes some animals more thermotolerant than others.

Genetic variability of heat tolerance and genetic evaluations

Most of the studies designed to determine the genetic value of heat tolerance of animals have focused on modeling the genetic component of performance under high heat loads as described by Ravagnolo et al. (2000). This approach describes the genetic component of the reaction to heat stress in performance with the so-called broken line model. The broken line model is defined by two parameters: 1) the thermoneutrality threshold and 2) the slope of decay in production after passing this threshold as a consequence of heat stress (Bernabucci et al., 2014). Alternatively, Brügemann et al. (2011), Menendex-Buxadera et al. (2012), and Carabaño et al. (2014) proposed the use of polynomials of second or third order to describe the norm of reaction of milk production across the heat load scale. Polynomial functions provide a more flexible approach than broken line models and allow for a smoother transit from thermotolerance to heat stress, instead of an abrupt change after the thermoneutrality threshold in broken line models. With this approach, steeper slopes at higher temperatures are accommodated, instead of a constant slope of decay in the broken line model, as might be expected to occur in reality. Reaction norm models using performance (both productive or reproductive) records and meteorological information have been extensively applied to measure heat tolerance in dairy or meat oriented production (Menéndez-Buxadera et al., 2012; Biffani et al., 2016; Bradford et al., 2016). One of the main issues in the application of this approach is how to combine climate variables in the models to define the amount of heat load that is received by the animals. A number of studies have dealt with the use of alternative definitions of indices that combine temperature, humidity and additional meteorological variables such as wind speed or insulation (Gaughan et al., 2012). The definition of the lag between the date of recording the animal's performance and the date for which weather conditions better determine the subsequent animal's response in performance has the same importance as the weather variables to be included in a heat load index (Bernabucci et al., 2014, Carabaño et al., 2014, Ramón et al., 2016). Another important issue is to determine the selection criteria derived for each model. In the broken line model, both the thermotolerance threshold and the slope of response of each individual could be used as selection criteria. However, the estimation of individual thresholds has been found to be troublesome from a computational point of view (Sánchez et al., 2009). Most applications of this model assign a predetermined value for the threshold and only the slope is estimated for each animal. The large estimated genetic correlation between threshold and slope [−0.95 in Sánchez et al. (2009)] indicates that selecting animals with less negative slope of response under heat stress will also result in higher thermotolerance thresholds. When higher than first-order polynomials or other functions are used to describe the norm of reaction to heat stress, the definition of selection criteria is less obvious. Alternative selection criteria might be the slope of the individual polynomial curves under moderate or severe heat stress or principal component values derived from the eigen decomposition of the covariance matrix of the random regression coefficients for the genetic component (Carabaño et al., 2014; Macciotta et al., 2017). All mentioned studies dealing with estimation of the genetic component of productive response under heat stress have shown variability across animals, indicating that genetic selection is possible. Figure 1 shows the estimated genetic deviation from the mean response to increasing temperatures of top, average, and bottom cows sorted by the level of milk, fat, protein, and somatic cell count using a broken line model. The figure illustrates the variability in genetic response of several animals and the reranking of animals at different temperatures, which indicates a certain degree of genotype by environment interaction. It can also be observed in this figure that the top animals for the level of the trait tend to show larger decays that an average animal, while the worst animals tend to have less negative responses than the average, which represents the antagonism between productivity and heat tolerance. The degree of antagonistic relationship in different types of dairy populations is illustrated in Figure 2. This figure shows the correlation between the estimated values for level of production and the rate of production decay under heat stress in three dairy populations: Holstein dairy cattle, the international breed Assaf and the local breed Manchega of dairy sheep. For the Holstein, which has been very intensively selected for milk production, correlations between milk production potential and the rate of production decay at successively higher temperatures becomes nearly −1 under heat stress, meaning that animals with a larger potential to produce milk will be the ones showing more negative slopes of decay. In contrast, these correlations are much lower for both sheep breeds, which implies that animals with an overall high potential for production and good heat tolerance is cumbersome. Selection indices with appropriate weighing for production and heat tolerance might be used to overcome the antagonistic relationship between those two traits. However, determining the appropriate economic weight for heat tolerance may be complex because of the difficulty of identifying all the animal performance parameters that are altered by heat stress and quantifying the associated economic loss.

Determination of the genetic component for other measures of heat tolerance has been mainly focused on body

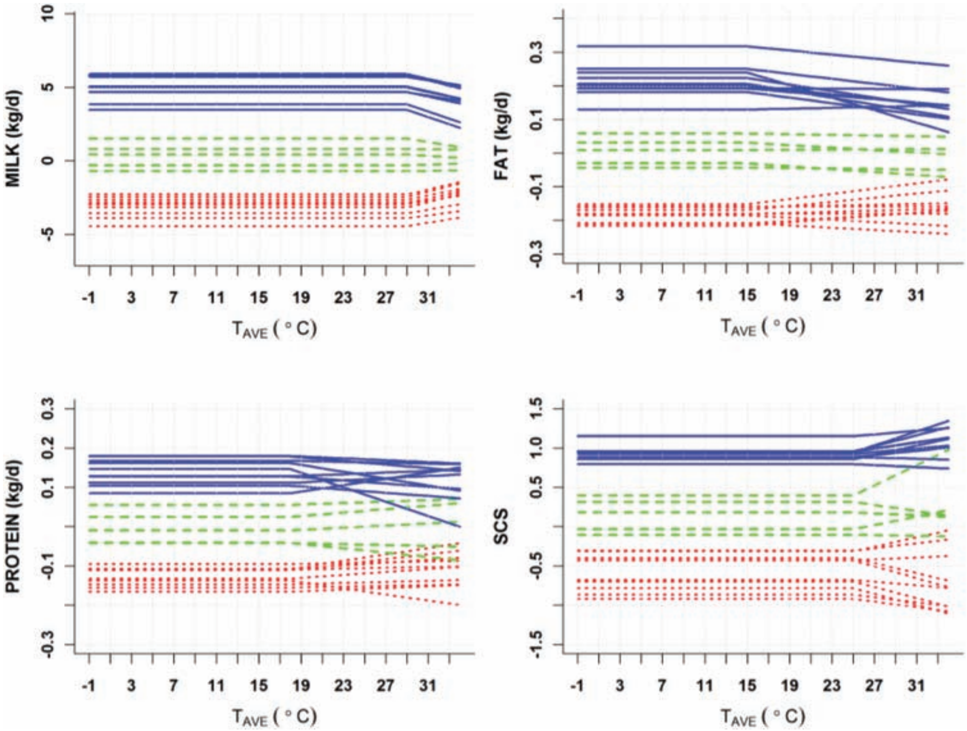

Figure 1. Estimated individual deviations from the average population response in productive traits, milk, fat, protein and somatic cell score (SCS), to increasing values of daily average temperature (T_{AVE}) under a broken line model for top (blue), average (green) and bottom (red) animals according to the level of each trait (Source: Carabaño et al., 2014).

temperature and respiration rate (Dikmen et al., 2012; Gourdine et al., 2017; Van Goor et al., 2016). The heritability estimates ranged from 0.10 for cloacal temperature in chicken and 0.17 in the dairy cattle study for rectal temperature to values more than 0.30 for both rectal or skin temperatures and respiration rate in lactating sows. Genetic variability has also been detected for this type of measure of heat tolerance, making selection theoretically feasible but impractical because of the high cost of measuring these parameters.

Overall, up to now, the attempts to produce genetic evaluations to select heat-tolerant animals have been based on analyses of performance under heat stress. Examples of these attempts can be found for dairy (Bohmanova et al., 2005) and beef cattle (Bradford et al., 2016). More recently, a genomically enhanced evaluation has been developed for dairy cattle in Australia (Nguyen et al., 2016).

Omics to understand the genetic component of heat tolerance

Quantitative genetic studies suggest a non-negligible genetic component of thermotolerance, which somehow is reinforced by a number of studies including "omic" information to gain knowledge about the genetic mechanisms behind the animal's response to heat. Three main types of studies can be found in the literature: 1) association studies of polymorphisms at specific genes and genome-wide association analysis (Macciotta et al., 2017); 2) genome comparison between adapted and nonadapted breeds/species to harsh environments (Chan et al., 2010) and 3) differential expression analyses (Chauhan et al. 2014). A literature review of these studies has provided over 431 candidate genes for the heat stress response. Results from a functional analysis of those genes using Panther v.11 (Mi et al., 2017) is shown in Figure 3. In general, genes reported for all three types of studies are functionally classified into similar

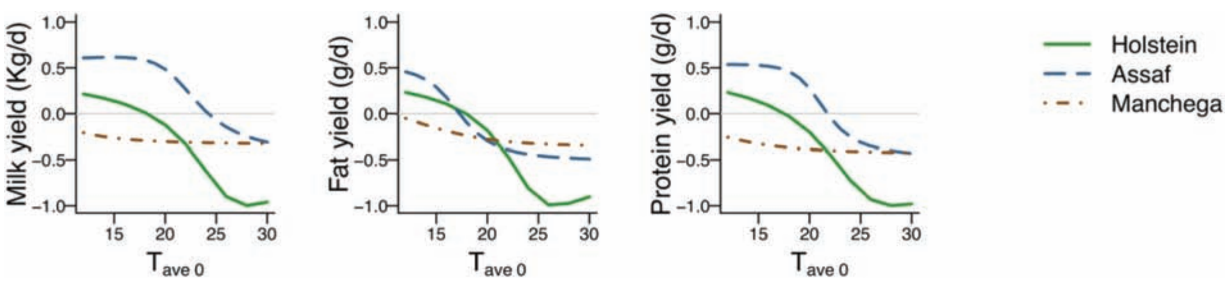

Figure 2. Correlations between estimated values for production level (milk, fat and protein yields) and thermo-tolerance (slope of production decay) along the scale of average daily temperatures (T_{ave0}) in three dairy breeds: Holstein cattle, International Assaf and Local Manchega sheep.

gene ontology terms which is a form of validating that the association analysis are pointing to the correct genomic regions (i.e., the ones that show differential expression under heat stress vs. thermoneutrality). Moreover, the pseudo-phenotypes used to measure heat tolerance and defined in different species for association studies are good proxies and are able to capture the sensitivity of animals to heat loads.

In Figure 3, biological processes are described by their outcome or ending states that are normally achieved by a set of molecular functions carried out by specific gene products. As part of the biological processes, those related with response to stress, as well as metabolic processes, biological regulation, or immune responses are the most represented. The heat stress response has been previously shown to result in increased catabolism, oxidative stress, and jeopardized immune response (Bernabucci et al., 2010), which agrees with the proposed candidate genes and their ontology.

Apart from the functional analysis of candidate genes for regulation of the heat stress response, we want to highlight families of genes that are present in association and differential expression studies. The most represented families are the heat shock proteins and DnaJs. DnaJs proteins seem to be crucial partners of the heat shock protein-70 (Qiu et al., 2006) and they are important for protein translation, folding, unfolding, translocation, and degradation. In addition, genes from interleukin, chemokine, and fibroblast growth factor families are found. These families are mostly involved in immunological and inflammatory processes, which are one of the major consequences for animals exposed to harsh environments (Bernabucci et al., 2010). Interestingly, heat shock factor-1 has also been found in several studies. Heat shock factor-1 is an evolutionarily conserved transcription factor that binds to the promoter regions of heat shock proteins to regulate their stress inducible synthesis in response to the environment. In summary, reports in the literature describe the complexity of the effects of heat stress on the physiology of a production animal and, therefore, illustrate the difficulties of using genomic information to select thermotolerant animals.

Apart from the numerous candidate genes that have been associated with regulation of the heat stress response, the slick

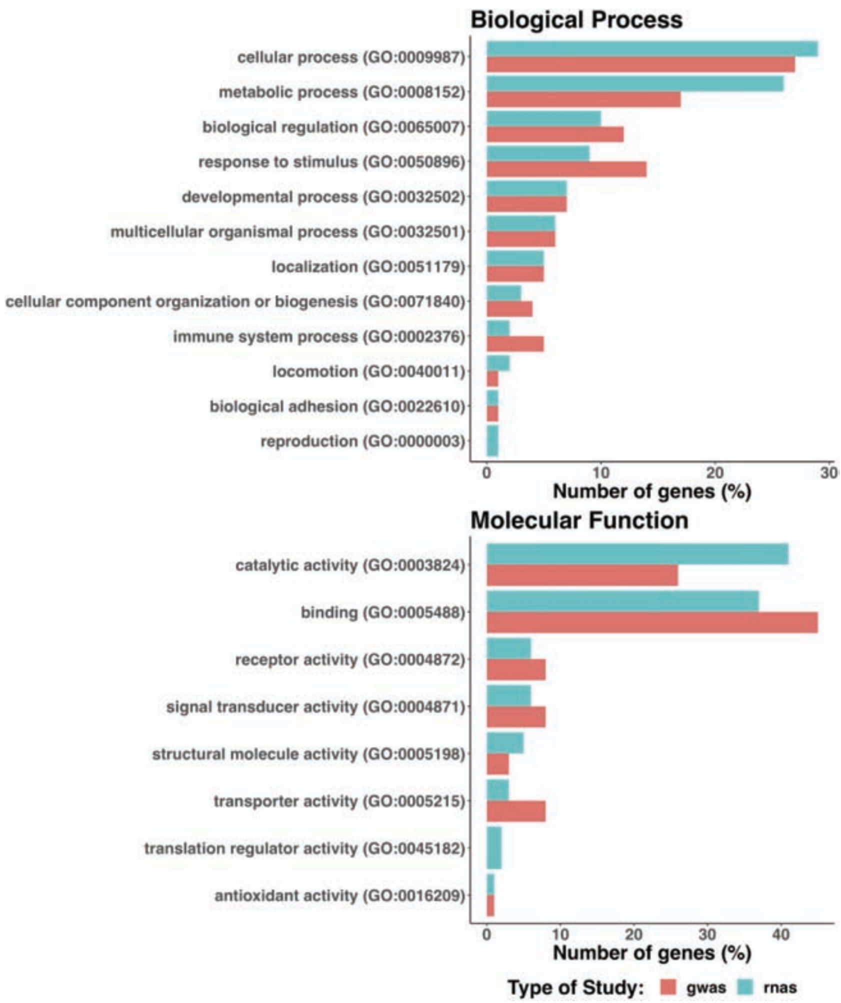

Figure 3. Gene ontology (GO) terms of genes reported in the literature of genome wide association (gwas) and transcriptomic (rnas) studies to be involved in the response of animals to heat stress. Bars show the number of genes (percent of total) for biological processes or molecular functions obtained from the GO analysis using Panther (http://pantherdb.org/).

hair gene deserves special attention. The slick hair gene, located on chromosome BTA20, is responsible for a smooth and short hair coat, confers thermotolerance to the animal, and is associated with an improved capacity for heat dissipation. Introgression of the slick hair gene (present in Senepol cattle and some lines of highly productive Holstein cattle) has been shown to produce animals with lower body temperatures and smaller declines in production under hot conditions (Dikmen et al., 2014; Ortiz-Colón et al., 2018). Slick positive Holstein bulls are already marketed by the artificial insemination companies. However, slick hair may decrease the ability of animals to cope with cold temperatures, which may be important in climates that include hot and cold periods.

Breeding Strategies

Breeds that originated in warm climates show adaptive advantages to heat stress compared with breeds that originated in temperate areas. Many studies have shown that under heat stress, breeds from warm climates have lower respiration rates, body temperature, or sweating rates and better reproductive performance than breeds from temperate climates (Hansen, 2004; Berman, 2011; Gourdine et al., 2017). Another general characteristic of locally adapted breeds is the low level of production. Berman (2011) and Hoffman (2010) reviewed the advantages and disadvantages of using breeds locally adapted to extreme conditions to improve tolerance to heat stress. One of the conclusions of Berman (2011) is that low productivity of adapted breeds might be a constitutional characteristic of these breeds since several studies show that breeds from warm climates and their crosses with selected breeds tend to favor fat deposition and body condition score over milk production when improved feeding is provided. The fact that fat deposition might be an advantageous constitutive characteristic associated with large seasonal variations in grazing conditions normally present in warm climates could be the evolutionary reason for this adaptation strategy. If this were the case, improving productivity in breeds adapted to harsh conditions might be impaired by this characteristic, and, on the other hand, the use of these breeds to improve heat tolerance of selected breeds might confer an undesirable genetic background in addition to the desired heat tolerance. Moreover, the enormous gap in productivity between selected and locally adapted breeds questions the profit from using these breeds to improve thermotolerance of more productive breeding stock when farm resources and animal health are not limiting the survival of highly selected breeds.

Overall, there are two main scenarios. When the production system is sufficient to provide adequate feeding, management, heat mitigation, and controlled parasite and pathogenic environment, selection for heat tolerance within highly productive breeds is likely to offer far more opportunity than improving local breeds. On the other hand, crossing of local and selected breeds and selection for productivity and monitoring of heat tolerance seems to be the best option to improve productivity in production systems that cannot provide mitigation for heat, adequate nutritional conditions or control of parasites and other pathogens. Figure 4 illustrates the results of current selection programs on milk production and heat tolerance (slope of production decay) in two populations of dairy cattle: 1) Holsteins raised in Mediterranean conditions (Carabaño et al., 2017) and 2) Gyr in the tropics (Santana et al., 2015). For both populations, genetic selection to increase milk production has had an associated negative response in the animal's ability to cope with heat stress. Similar results have been shown in Carabaño et al. (2017) for local goat and sheep breeds in Spain. Thus, even for locally adapted breeds, heat tolerance has to be monitored when selection for productivity is implemented in production systems affected by heat stress.

Conclusions

Heat stress is a complex phenomenon that triggers a number of response mechanisms in animals that have a negative effect on farm profitability. Of all the actions that farmers can implement to adapt to the challenge of heat stress, genetic selection can provide a cost-effective and efficient tool to improve the resilience of farms to hot conditions. Up to now, selection procedures were based on estimating the decrease in

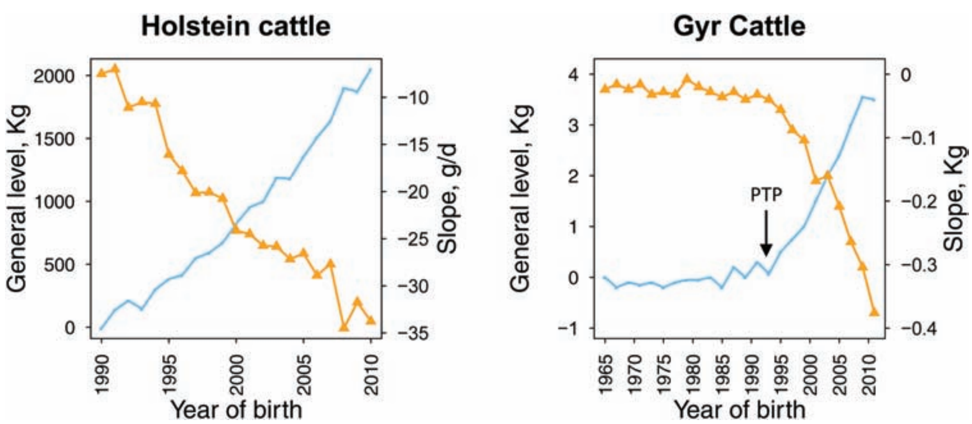

Figure 4. Estimated genetic trends in two dairy cattle breeds: Holstein (*Bos Taurus*) amd Gyr (*Bos indicus*). Lines show genetic trends for milk production (blue) and heat tolerance (orange). For Gyr cattle, year of first result of progeny test program (PTP) is marked by and arrow. Source: Carabaño et al., 2017 (left) and Santana et al., 2015 (right).

production under heat stress by using information from current farm recording schemes and meteorological information on the day of recording. Substantial genetic variability has been observed in an individual animal's response to increased heat loads, with a moderate degree of genotype by environment interaction, which implies that animals that are the best producers under comfort may not be the best animals under heat stress. However, this approach has two major drawbacks: 1) inaccuracy of the individual estimate of the animal's ability to maintain its level of productivity under heat stress because of the scarcity of individual records along the heat load scale and 2) antagonism between the productive and heat tolerance criteria. Thus, it is necessary to improve heat tolerance phenotyping to produce more accurate measures to identify heat tolerant animals and increase our understanding of the underlying genetic mechanisms of heat tolerance that can be used in selection programs.

A large amount of knowledge is being accumulated about the underlying mechanisms of the heat stress response from "omics" studies. Many candidate genes and potential biomarkers have been proposed from DNA, RNA, and metabolomics studies, but there is still work to be done to combine this accumulated knowledge to provide selection tools to improve heat tolerance in breeding schemes.

Optimal breeding strategies to improve heat tolerance of livestock (i.e., selecting for heat tolerance within highly productive populations vs use crossbreeding or introgression involving local and selected breeds) will depend on the farm resources (including nutrition, management, and investment capacity) and level of parasite or other pathogen challenges of the production system.

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Feature Article

Livestock and climate change: impact of livestock on climate and mitigation strategies

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Implications

- The livestock sector requires a significant amount of natural resources and has an important role in global greenhouse gas emissions. The most important greenhouse gases from animal agriculture are methane and nitrous oxide.
- Mitigation strategies aimed at reducing the emission intensity of this sector are needed to meet the increasing demand for livestock products driven by population growth.
- To increase the effectiveness of mitigation strategies, the complex interactions among the components of livestock production systems must be taken into account to avoid environmental trade-offs.

Key words: climate change, greenhouse gases, livestock, mitigation

Introduction

According to the United Nations (UN, 2017), the world population increased by approximately 1 billion inhabitants during the last 12 years, reaching nearly 7.6 billion in 2017. Although this growth is slower than 10 years ago (1.24% vs. 1.10% per year), with an average increase of 83 million people annually, global population will reach about 8.6 billion in 2030 and 9.8 billion in 2050. Population growth, urbanization, and income rise in developing countries are the main driver of the increased demand for livestock products (UN, 2017). The livestock sector requires a significant amount of natural resources and is responsible for about 14.5% of total anthropogenic greenhouse gas emissions (7.1 Gigatonnes of carbon dioxide equivalents for the year 2005; Gerber et al., 2013). Mitigation strategies aimed at reducing emissions of this sector are needed to limit the environmental burden from food production while ensuring a sufficient supply of food for a growing world population. The objectives of this manuscript are to 1) discuss the main greenhouse gas emissions sources from the livestock sector and 2) summarize the best mitigation strategies.

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Impact of Livestock on Climate Change

The most important greenhouse gases from animal agriculture are methane and nitrous oxide. Methane, mainly produced by enteric fermentation and manure storage, is a gas which has an effect on global warming 28 times higher than carbon dioxide. Nitrous oxide, arising from manure storage and the use of organic/inorganic fertilizers, is a molecule with a global warming potential 265 times higher than carbon dioxide. The carbon dioxide equivalent is a standard unit used to account for the global warming potential (IPCC, 2013).

Figure 1 was adapted from the Global Livestock Environmental Assessment Model (GLEAM) developed by FAO (FAO, 2017) and shows in carbon dioxide equivalents the greenhouse gas incidences that enteric fermentation and manure storage have across the main livestock species raised worldwide.

In addition to greenhouse gases arising from enteric fermentation and manure storage, feed production together with the related soil carbon dioxide and nitrous oxide emissions is another important hot spot for the livestock sector. Soil carbon dioxide emissions are due to soil carbon dynamics (e.g., decomposing plant residues, mineralization of soil organic matter, land use change, etc.), the manufacturing of synthetic fertilizers and pesticides, and from fossil fuel use in on-farm agricultural operations (Goglio et al., 2018). Nitrous oxide emissions are emitted when organic and inorganic fertilizers are applied to the soil.

As shown in Figure 2, feed production and processing contribute about 45% of the whole sector (3.2 Gigatonnes of carbon dioxide equivalents). Enteric fermentation producing about 2.8 Gigatonnes (39%) is the second largest source of emissions. Manure storage with 0.71 Gigatonnes accounts for about 10% of the total. The remaining 6% (0.42 Gigatonnes of carbon dioxide equivalents) is attributable to the processing and transportation of animal products (Gerber et al., 2013).

Feed production (Figure 2) includes all the greenhouse gas emission arising from 1) land use change, 2) manufacturing and use of fertilizers and pesticides, 3) manure excreted and applied to fields, 4) agricultural operations, 5) feed processing, and 6) feed transport. Although these processes result in a large share of the livestock supply chain, in this article, we mainly focus on direct livestock emissions enteric fermentation, manure storage, and manure excreted/applied to the soil. All other emissions are outside the scope of this article.

Enteric fermentation

Enteric fermentation is a natural part of the digestive process of ruminants where bacteria, protozoa, and fungi contained in the fore-stomach of the animal (rumen), ferment and break down the plant biomass eaten by the animal. Plant biomass in the rumen is converted into volatile fatty acids, which pass the rumen wall and go to the liver through the circulatory system. This process supplies a major part of the energy needs of the animal and enables the high conversion efficiency of cellulose and semi-cellulose, which is typical of ruminants. The gaseous waste products of enteric fermentation, carbon dioxide and methane, are mainly removed from the rumen by eructation. Methane emission in the reticulorumen is an evolutionary adaptation that enables the rumen ecosystem to dispose hydrogen, which may otherwise accumulate and inhibit carbohydrate fermentation and fiber degradation (McAllister and Newbold, 2008). The emission rate of enteric methane varies according to feed intake and digestibility.

Manure storage

Manure acts as an emission source for both methane and nitrous oxide, and the quantity emitted is linked to environmental conditions, type of management and composition of the manure. Organic matter and nitrogen content of excreta are the main characteristics influencing emission of methane and nitrous oxide, respectively. Under anaerobic conditions, the organic matter is partially decomposed by bacteria producing methane and carbon dioxide. Storage or treatment of liquid manure (slurry) in a lagoon or tank promotes an anaerobic environment which leads to an increase in methane production. Long storage periods and warm and wet conditions can further increase these emissions (EPA, 2010). On the other hand, nitrous oxide emissions need a combination of aerobic and anaerobic conditions to be produced. Therefore, when manure is handled as a solid (dung) or deposited on pastures, nitrous oxide production increases while little or no methane is emitted. Nitrous oxide is generated through both the nitrification and denitrification processes of the nitrogen contained in manure, which is mainly present in organic form (e.g., proteins) and in inorganic form as ammonium and ammonia. Nitrification occurs aerobically and converts ammonium and ammonia to nitrites and then nitrates, while denitrification occurs anaerobically converting nitrates to nitrous oxide and

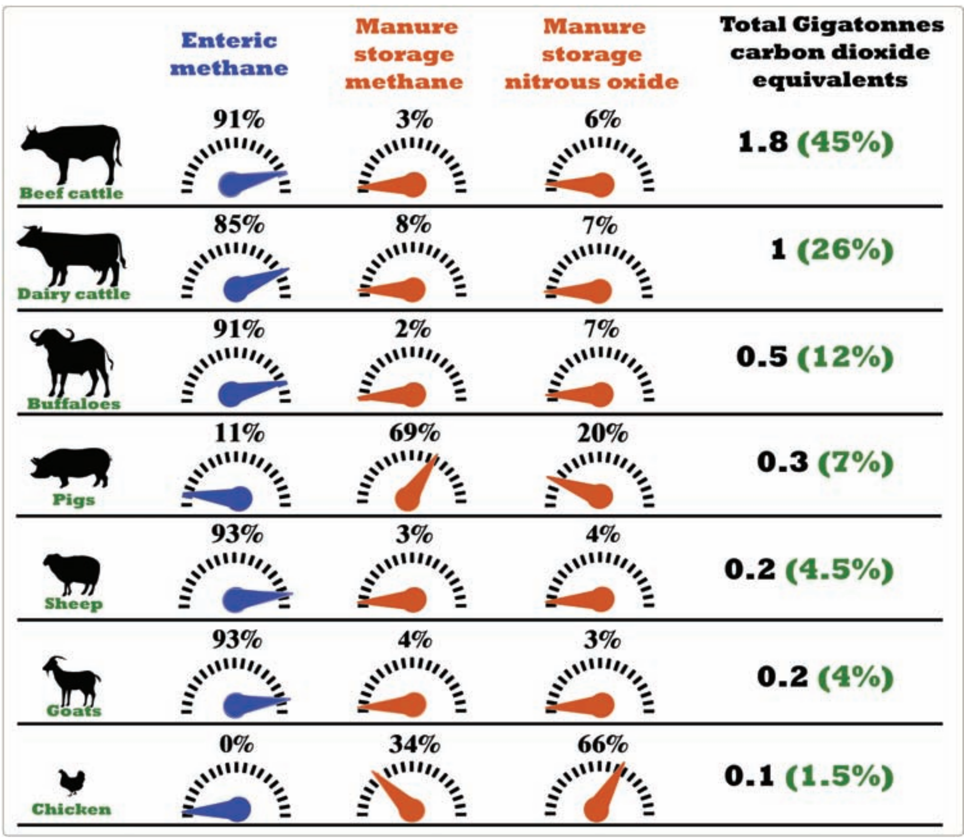

Figure 1. Greenhouse gases incidence of enteric fermentation and manure storage by animal type, expressed as Gigatonnes of carbon dioxide equivalents. Data referred to 2010 (FAO, 2017).

nitrogen gas (Saggar, 2010). The balance between ammonium and ammonia is highly affected by pH, with ammonia increasing as pH increases.

Feed production

Almost 60% of the global biomass harvested worldwide enters the livestock subsystem as feed or bedding material (Krausmann et al., 2008). Greenhouse gas emissions from feed production represent 60–80% of the emission coming from eggs, chicken and pork, and 35–45% of the milk and beef sector (Sonesson et al., 2009). As shown in Figure 2, emissions from feed production account for about 45% of the livestock sector. The application of manure as fertilizer for feed crops and the deposition of manure on pastures generates a substantial amount of nitrous oxide emissions representing about half of these emissions (Gerber et al., 2013). Although livestock feed production often involves large applications of nitrogen to agricultural soils, good manure management can reduce the need for manufactured fertilizers.

Livestock Mitigation Strategies

The extreme heterogeneity of the agricultural sector needs to be taken into account when defining the overall sustainability of a mitigation strategy, which can vary across different livestock systems, species, and climates. Generally, no measure in isolation will encompass the full emission reduction potential, while a combination selected from the full range of existing options will be required to reach the best result (Llonch et al., 2017). It is also important to consider the "pollution swapping" effect when evaluating the effectiveness of a mitigation strategy (Hristov et al., 2013). Reduction of methane emissions during enteric fermentation might be counteracted by increased greenhouse gas emissions in applied manure. Reduction of direct nitrous oxide emissions during storage might result in higher nitrate leaching and ammonia volatilization during field application.

Mitigation may occur directly by reducing the amount of greenhouse gases emitted, or indirectly through the improvement of production efficiency. The main strategies to mitigate greenhouse gas emissions in the livestock sector have been investigated and are summarized in Table 1.

Enteric fermentation

Decreasing methane emissions from ruminants is one pressing challenge facing the ruminant production sector. Strategies for reducing this source of emissions focus on improving the efficiency of rumen fermentation and increasing animal productivity. A large number of mitigation options have been proposed (e.g., diet manipulation, vaccines, chemical additives, animal genetic selection, etc.) with different efficiencies in reducing enteric methane as shown in Table 1.

Forage quality and digestibility affect enteric methane production. Lignin content increases during plant growth, consequently reducing plant digestibility. Therefore, harvesting forage (especially grass) for ensiling at an earlier stage of maturity increases its soluble carbohydrate content and reduces lignification. According to Knapp et al. (2014) practices aimed to increase forage quality have shown a potential enteric methane reduction of about 5% per unit of fat protein corrected milk.

Physical processing of forages, such as chopping, grinding, and steam treatment, also improves forage digestibility and mitigates enteric methane production in ruminants (Hristov et al., 2013). However, the reduction potential of this practice

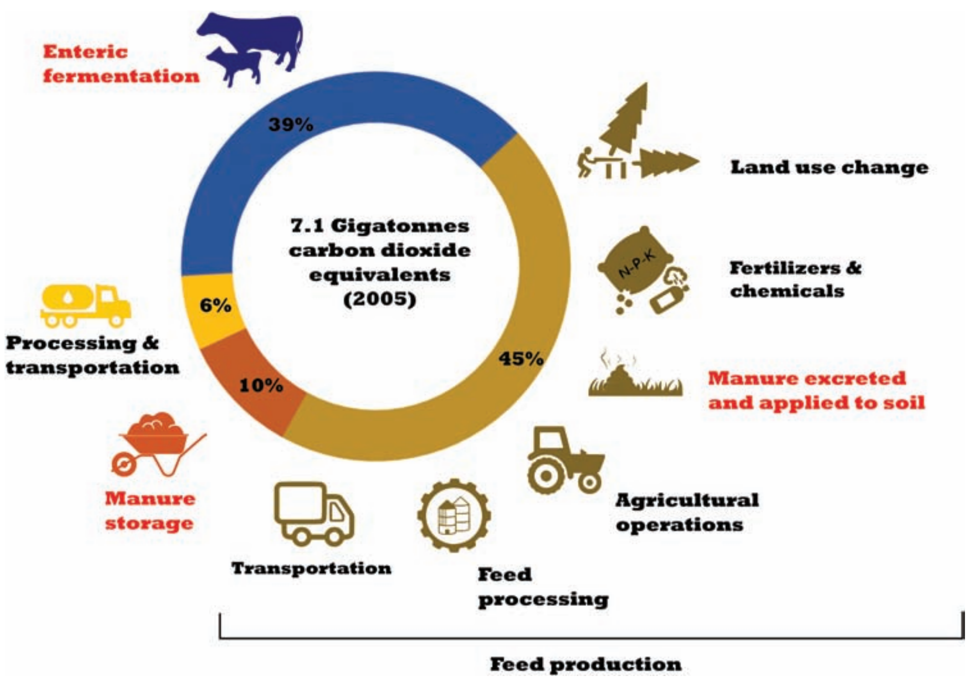

Figure 2. Livestock emissions by source (adapted from Gerber et al., 2013). Direct livestock emissions are shown in red.

Table 1. Mitigation potential of various strategies

Strategies	Category	Potential mitigating effect*	
		Methane	Nitrous Oxide
Enteric fermentation	Forage quality	Low to medium	†
	Feed processing	Low	Low
	Concentrate inclusion	Low to medium	†
	Dietary lipids	Medium	†
	Electrons receptors	High	†
	Ionophores	Low	†
	Methanogenic inhibitors	Low	†
Manure storage	Solid-liquid separation	High	Low
	Anaerobic digestion	High	High
	Decreased storage time	High	High
	Frequent manure removal	High	High
	Phase feeding	‡	Low
	Reduced dietary protein	‡	Medium
	Nitrification inhibitors	‡	Medium to high
	No grazing on wet soil	Low	Medium
	Increased productivity	High	High
Animal management	Genetic selection	High	‡
	Animal health	Low to medium	Low to medium
	Increase reproductive eff.	Low to medium	Low to medium
	Reduced animal mortality	Low to medium	Low to medium
	Housing systems	Medium to high	Medium to high

*High = ≥30% mitigating effect; Medium = 10–30% mitigating effect; Low = ≤10% mitigating effect. Mitigating effects refer to percent change over a "standard practice" according to Newell Price et al. (2011); Borhan et al. (2012); Hristov et al. (2013); Montes et al. (2013); Petersen (2013); Battini et al. (2014); Knapp et al. (2014); Llonch et al. (2017); Mohankumar Sajeev et al. (2018).

†Inconsistent/variable results.

‡Uncertainty due to limited research or lack of data.

was reported to be less than 2% per unit of fat protein corrected milk (Knapp et al., 2014).

Improving diet digestibility by increasing concentrate feeding is another effective mitigation strategy, reducing by 15% methane emissions per unit of fat protein corrected milk (Knapp et al., 2014). However, the ratio of forage to concentrate has to be carefully taken into account when applying this strategy. Indeed, although a marked reduction of enteric methane can be expected with rates of concentrate inclusion between 35% and 40% (Gerber et al., 2013). A greater proportion of dietary fermentable carbohydrates could increase the risk of metabolic diseases (e.g., rumen acidosis).

Addition of fats or fatty acids to the diets of ruminants can decrease enteric methane emissions by both decreasing the proportion of energy supplied from fermentable carbohydrates and changes in the microbial population of the rumen (Llonch et al., 2017). Although some byproducts (e.g., cottonseed, brewer's grains, cold-pressed canola meal, etc.) are effective in reducing enteric fermentation (Moate et al., 2011), the mitigation potential of high oil byproducts has not been well-established and in some cases methane production may increase due to increased fiber intake (Hristov et al., 2013). The inclusion of lipids higher than 10% can lead to impairment of ruminal function due to changes to the microbial population which in turn decreases the ability to digest fiber. Lipid diet supplementation between 5% and 8% of the dry matter intake is an effective mitigation strategy (Grainger and Beauchemin, 2011) with a potential enteric methane reduction of about 15% per unit of fat protein corrected milk (Knapp et al., 2014).

Feed additives (electron receptors, ionophoric antibiotics, chemical inhibitors, etc.) have also been tested for their ability to decrease methane emissions (Beauchemin et al., 2009). However, the unknown toxicity and the health risks associated with the use of some of these compounds may severely constrain widespread adoption (Herrero et al., 2016).

Manure storage

Increased animal density together with continuous inflow of nutrients from imported feeds is likely to increase volumes of manure to be managed. Stored manure accounts for a relatively small amount of direct agricultural greenhouse gases (Figure 2), and it is technically possible to mitigate a very high percentage of these emissions (Hristov et al., 2013). In the following section, some of the most effective mitigation strategies are discussed.

As methane production increases with the temperature of stored manure, a reduction of storage temperature has been reported to drop these emissions by 30–50% (Borhan et al., 2012). However, the net greenhouse gas mitigation resulting from this strategy can vary widely, and it is strictly related to the energy used and the cooling system adopted.

Frequent removal of manure to an outside storage facility is an effective practice that can be accomplished using grooved floors combined with regular scraping of manure, especially for pigs and some cattle production systems. Indeed, if the channels underneath the stable are emptied regularly, and the manure/slurry are transported to an outside storage facility, this practice has the potential to reduce methane and nitrous oxide emissions by 55% and 41%, respectively (Mohankumar Sajeev et al., 2018). On poultry farms the litter/manure is usually removed at the end of the crop; however, advanced layer housing using belt scrapers can efficiently remove litter/manure continuously and decrease greenhouse gas emissions (Fournel et al., 2012).

Solid-liquid separation is a processing technology that partially separates the solids from liquid manure using gravity or mechanical systems such as centrifuges or filter presses. As shown in Table 1, the greenhouse gas mitigation potential of this technique has been reported to be higher than 30% compared with untreated manure (Montes et al., 2013). The organic component with a larger particle size follows the solid stream during the separation process, and it is then stored in stockpiles. The aerated condition of the storage can then limit the potential for methane to be emitted; however, ammonia loss through composting and generating high temperatures can be accelerated. Also, the remaining liquid fraction is still a potential source of indirect nitrous oxide emissions. Indeed, once the fibrous and large pieces of organic material are subtracted, it will not form a crust during storage, leading to increased volatilization of ammonia by increasing the mass transfer coefficient at the surface. Although greenhouse gas mitigation of the solid-liquid separation process can be partially counterbalanced by ammonia emissions, it is important to note that there are many management practices that can overcome these issues, such as covering slurry storage and the use of injection for land application (Holly et al., 2017).

Anaerobic digestion is a biological degradation process, which in the absence of oxygen, produces digestate and biogas (mainly methane and carbon dioxide) from manure. Biogas collected from the system is often used to generate electricity, to fuel boilers or furnaces, or to provide combined heat and power. Taking into account the greenhouse gas emissions arising from the use of the digestate as fertilizer, and the credit for the renewable energy produced, anaerobic digestion has been reported to yield more than 30% reduction in greenhouse gas emissions when compared with traditional manure handling systems (Battini et al., 2014). However, further attention to the management of the digestate leaving the anaerobic digestion is needed. Indeed, mineralization of the organic nitrogen occurring during biological degradation increases the inorganic nitrogen content and pH of the effluent, which in turn may increase ammonia volatilization (Petersen and Sommer, 2011). Combining anaerobic digestion and solid-liquid separation could reduce the amount of ammonia lost following digestion (Holly et al., 2017).

Diet severely affects excretion of nitrogen in most farm animals, therefore grouping livestock on the basis of their feed requirements can help in reducing this source of nitrous oxide in the excreta. Although a low-protein diet could effectively mitigate nitrous oxide emissions from cattle manure storage (Table 1), some attention must be given to manipulating dietary nitrogen (Montes et al., 2013). For example, decreasing protein could lead to an increase of fermentable carbohydrates, which in turn will likely increase methane production.

The diet for all animal species should be balanced for amino acids to avoid a depression in feed intake and a decrease in animal productivity. Manufactured amino acids are routinely used to balance the diet of monogastrics (pigs and poultry), but the environmental impact associated with the manufacturing of these supplements must be considered when including amino acids as a greenhouse gas mitigation strategy. In ruminants, supplementation of free amino acids results in fast degradation in the rumen, without a significant increase in animal productivity. On the contrary, rumen-protected amino acids resist chemical alterations in the rumen and can reach the intestine where they are absorbed, improving milk yield in dairy cows. Overall, feeding protein close to the animal's requirement is recommended as an effective mitigation strategy to reduce ammonia and nitrous oxide emissions from manure (Montes et al., 2013).

Feed production

The timing, quantity, and method of fertilizer applications are important factors influencing soil nitrous oxide emissions. The nitrogen fertilizer applied is susceptible to loss by leaching and denitrification before crop uptake. Therefore, ensuring that appropriate amounts of nitrogen get to the growing crop and avoiding application in wet seasons or before major rainfall events, are valuable practices which could help in optimizing biomass production and reduce soil greenhouse gas emissions.

As lower methane emissions occur after manure land application, decreasing storage time can effectively help in reducing greenhouse gas emissions (Table 1). However, the resulting frequent soil applications can have a variable effect on nitrous oxide emissions from field and carbon dioxide emissions from fuel combustion. Avoiding application during prolonged periods with wet soil and periods of low plant nitrogen uptake could help in increasing the effectiveness of this practice (Hristov et al., 2013).

Adequate storage facilities can provide greater flexibility in choosing when to apply manure to fields, while the use of on-farm manure analysis could help the farmer develop a nutrient management plan and minimize environmental impacts (Newell Price et al., 2011).

The use of nitrification inhibitors has the potential to reduce nitrogen leaching by inhibiting the conversion of ammonia to nitrate. However, this beneficial effect is weakened by a reported increase in indirect nitrous oxide emission that can result from increased ammonia volatilization (Lam et al., 2016). This highlights the importance of considering both gases when evaluating the use of nitrification inhibitors as an option to mitigate climate change. Overall, nitrification inhibitors have been demonstrated as an effective practice to reduce nitrous oxide emissions (Table 1).

Intensive rotational grazing systems are being promoted as a good way to increase forage production and reduce nitrous oxide emissions (Table 1). These systems are characterized by multiple smaller fields called paddocks for the rotation of livestock. By subdividing pastures and rotating animals, farmers can manage stocking densities and grazing duration and thereby manage nitrogen excreta distribution and vegetation regrowth. A more uniform distribution of urine throughout the paddock would reduce the effective nitrogen application rate, which could translate into a reduction in nitrous oxide emissions (Eckard et al., 2010). Keeping animals off the paddocks during wet weather will reduce sward damage and soil compaction. In addition, avoiding excreta deposition at these times will reduce nitrous oxide emissions and nitrogen leaching (Luo et al., 2010).

Animal management

There is a direct link between greenhouse gas emission intensities and animal efficiency. The more productive the animal is, the lower the environmental impact will be (on a per unit of product basis). Both management quality and expression of full genetic potential are necessary to increase production efficiency.

Breeding for more productive animals can lead to a reduction of the nutrient requirements needed to reach the same level of production. This is a valuable greenhouse gas mitigation strategy (Table 1). A more efficient animal will retain more dietary nitrogen protein and there will less nitrogen in feces and urine (Gerber et al., 2013). Genetic improvement of daily gain and feed conversion that has been achieved in broilers over the last 20 years has reduced substantially the emissions per unit of weight (Williams and Speller, 2016). Nevertheless, strategies that aim to change animal phenotypes to enhance productivity or efficiency may harm animal health and welfare unless these effects are measured and controlled (Llonch et al., 2017). Animals of a particular genotype selected for increased production will only be able to realize this potential on a high input system in which resources are adequately supplied. In other words, new breeds and crosses can lead to substantial greenhouse gas reduction, but they need to fit within production systems and climates that may be characterized by limited resources and other constraints.

Poor fertility means that more breeding animals are required in the herd to meet production targets, and more replacements are required to maintain the herd size, which in turn increases greenhouse gas emissions. Improved fertility in dairy cattle could lead to a reduction in methane emissions by 10–24% and reduced nitrous oxide by 9–17% (Table 1). Nevertheless, increasing reproductive pressure may increase the metabolic demands associated with pregnancy and lactation that could negatively affect animal health and increase the risk of metabolic diseases, reduce immune function and in turn reduce fertility (Llonch et al., 2017).

Poorer livestock health and welfare are associated with behavioral and metabolic changes, which can effect greenhouse gas emissions in several ways. Animals fighting an infection will need more energy for maintenance. A recent study in the United Kingdom investigated cost-effective ways to reduce greenhouse gas emissions by improving cattle health. These studies found that cattle diseases can increase greenhouse gas emissions up to 24% per unit of milk produced and up to 113% per unit of beef carcass (Williams et al., 2015). A disease that temporarily reduces feed intake or the ability to digest feed, leads to a decline in growth rate, which will result in more time and energy needed to reach the same end point.

Conclusion

Agriculture in general, and livestock production, in particular, contributes to global warming through emissions of methane and nitrous oxide. To meet future needs of an expanding population, animal productivity will need to increase and greenhouse gas emission intensity per unit of product will need to decrease. One of the principal ways to achieve this environmental standard is to adopt effective mitigation strategies. To increase the effectiveness of these strategies, complex interactions among the components of livestock production systems must be taken into account to avoid environmental trade-offs. Unfortunately, there is not a standard procedure to follow. Mitigation practices should not be evaluated individually, but as a component of the entire livestock production system. The majority of these strategies aim to increase productivity (unit of product per animal), which in most cases cannot be achieved without good standards of animal health and welfare. Optimizing animal productivity has a powerful mitigating effect in both developed and developing countries; however, the size of the effect will also depend on factors such as the genetic potential of the animal and adoption of management technologies.

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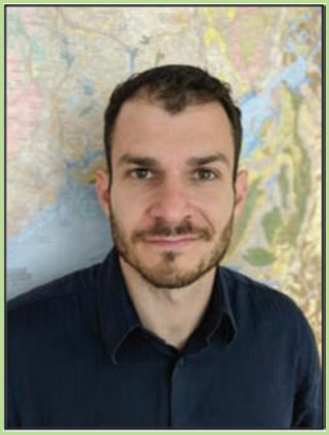
About the Authors



Giampiero Grossi is a PhD student in the Department of Agriculture and Forestry Science (DAFNE) at Tuscia University, Italy. His research is focused on the quantification of greenhouse gases arising from a typical agro-silvo-pastoral system of the Mediterranean area. Giampiero is currently applying life cycle assessment methodology to a case study in Castelporziano, Rome. His background encompasses agri-food environmental certifications, livestock management, and farming practices. **Corresponding author:** g.grossi@unitus.it

Pietro Goglio is a lecturer in life-cycle assessment and systems modeling at Cranfield University. He has a strong environmental background and has conducted research in the life-cycle analysis of agricultural and bioenergy systems. Currently, Dr Goglio is focusing his research on developing approaches to combine science with life cycle assessment approaches for greenhouse gas removal from the atmosphere and for greenhouse gas accounting for agricultural systems and food systems. These research developments aim to better capture the characteristics of the systems by considering the economic, social, and political factors affecting their performance and implementation.

Andrea Vitali is a lecturer in Sustainable Livestock Production in the master degree of Food Science and Technology at University of Teramo. His research focused on the bidirectional relationships between animals and the environment. He has studied the effects of heat stress on livestock (production, reproduction, and health) and the contribution of animals to global warming. He has expertise in the application of systems based life-cycle assessment to livestock production. He was involved in developing the Italian plan for adaptation to climate change related to agriculture and food production.

Adrian Williams has spent many years working in agri-environmental science. He is a leading expert in the application of systems based life-cycle assessment to agricultural and food production. He has studied the production of all major crop and livestock species in the United Kingdom and abroad (e.g., beef in Brazil). He has applied life-cycle assessment to the greenhouse gas benefits of improved cattle health as well as enhanced welfare in pig and poultry housing. He is responsible for developing the beef sector model in the recently enhanced agricultural greenhouse gas inventory in the United Kingdom.

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American Meat Science Association News

The American Meat Science Association (AMSA) fosters community and professional development among individuals who create and apply science to efficiently provide safe and high-quality meat.

AMSA Announces a New PORK 101 Course for 2019

The American Meat Science Association (AMSA) is excited to announce that a PORK 101 course will be held at the University of Florida March 4–6, 2019. With the addition of the course, we can expand the outreach of this valuable program and enable others to take advantage of the great opportunity to learn from our outstanding AMSA members.

PORK 101 is hosted by AMSA in cooperation with the National Pork Board and is sponsored by Merck Animal Health. Attendees will experience firsthand the swine industry from live animal production through finished pork products. The course concludes with the attendees preparing and sampling products from pork carcasses including pumped loins, bacon, hams, and sausage.

Attendees will have the opportunity to learn about the value differences in swine, pork carcasses, pork primals and processed pork products from meat science faculty and AMSA members at each university.

The program features:

- General Production Practices
- Hog Handling
- Grading and Live Hog Evaluation
- Lean Value Pricing
- Quality Management at Slaughter
- Hands-On Pork Slaughter
- Measuring Carcass Quality and Composition
- Hands-On Pork Carcass Fabrication
- Processing Technologies and Hands-On Lab
- Retail and Consumer Hot Topics

PORK 101 is co-sponsored by the American Association of Meat Processors (AAMP), North American Meat Institute Foundation (NAMIF), Southeastern Meat Association (SEMA),and the Southwest Meat Association (SMA). Registration for AMSA members and other partnering organizations is $825. Non-member registration is $975. Companies or organizations sending more than one person to the course are eligible for a discount! Space is limited for each course so make sure to register soon!

Past attendees of the AMSA PORK 101 Course can attest to the importance of attending.

- "The instructors were so accommodating and knowledgeable, and the course was very well structured. I would highly recommend this class to anyone and everyone in the meat industry – especially marketing or sales personnel."
- "I can speak to the entire process of how pork is harvested now. Understanding the primals and the bone-in/boneless cuts is very important in my role."
- "Great course! I felt like the hands-on cutting was a great learning tool where I grew more familiar with each of the cuts of pork."

For more information or questions regarding PORK 101 please visit: http://www.meatscience.org/events-education/pork-101 or contact Deidrea Mabry dmabry@meatscience.org.

AMSA Announces SALUMI 101 Course January 9–11, 2019

Registration for SALUMI 101 is now open and space will be limited so register early! SALUMI 101 will be held January 9–11 at California State University-Fresno in Fresno, CA. SALUMI 101 is sponsored by American Meat Science Association (AMSA), North Carolina State University, California State University – Fresno, Pennsylvania State University, and the University of Wisconsin-Madison.

A unique three-day, hands-on educational opportunity for all attendees, "Salumi 101 is great for trained chefs and serious cured meat processors alike. The equal time between hands on training and in-depth classroom curriculum was fantastic. I thoroughly enjoyed all the teachers and staff," stated a past attendee.

Anyone with a passion for learning more about the art and science of crafting high quality artisan meat products will benefit from attending SALUMI 101. This workshop will give participants the chance to interact with industry, and university professionals that specialize in this area of meat science. Participants will learn about the production of safe and high-quality artisan-style meat products as well as be involved with the crafting of various artisan products. More information is posted online.

Join AMSA Today and Save!

AMSA members receive discounts on registration fees for the AMSA Reciprocal Meat Conference, PORK 101, and many other AMSA co-sponsored short courses focusing on meat science and an invitation to attend the International Congress of Meat Science and Technology (ICoMST). To see all the AMSA member benefits and to join AMSA please visit: http://www.meatscience.org/Membership/.

2019 AMSA Calendar of Events

January 9–11: SALUMI 101 - California State University-Fresno (Fresno, CA)

doi: 10.1093/af/vfy032

January 20: National Western Intercollegiate Meat Judging Contest (Greeley, CO)
February 3: Southwestern Intercollegiate Meat Judging Contest (Fort Worth, TX)
February 9: Iowa State University Meat Evaluation Contest (Ames, IA)
February 11: PORK 101 Short Course – IPPE (Atlanta, GA)
February 22–24: Tyson Beyond Fresh Meat (Springdale, AR)
March 4–6: PORK 101 University of Florida (Gainesville, FL)
March 31-April 2: National Meat Animal Evaluation Contest, Oklahoma State University (Stillwater, OK)

Reciprocal Meat Conference 2019–2020

June 23–26, 2019: Colorado State University (Fort Collins, CO)
August 2–7, 2020: RMC and ICoMST; Disney Coronado Springs Resort (Lake BuenaVista, FL)

The American Society of Animal Science fosters the discovery, sharing and application of scientific knowledge for the responsible use of animals to enhance human life and well-being.

Best Wishes to Dr. James Sartin

Please join ASAS in extending best wishes to Dr. James Sartin, who is retiring as EiC of the *Journal of Animal Science* (2015-2018), *Animal Frontiers* (2015-2018) and *Translational Animal Science* (2017-2018). After serving ASAS as both an invaluable editor and President of ASAS, Dr. Sartin is stepping down as EiC to enjoy more time with his family and to pursue long term interests in retirement. Although we are excited for Dr. Sartin as he moves into this next phase, we are sad to see him leave.

Dr. Sartin has been integral in drastically improving *JAS* time to publication, transitioning the ASAS journals through two new publishers, co-founding TAS, and much more. To honor the contributions of Dr. Sartin, the ASAS Foundation has initiated an appreciation club in his name. You can donate to the Dr. James Sartin Appreciation Club, online at **asas.org**.

Dr. Sally Johnson

Dr. Deb Hamernik

Dr. James Oltjen

ASAS Welcomes new EiCs

With the retirement of Dr. Sartin, ASAS is pleased to announce the new editors for the *Journal of Animal Science*, *Animal Frontiers* and *Translational Animal Science*. Please join us in welcoming our new EiCs.

Journal of Animal Science – Dr. Sally Johnson, Virginia Tech

Animal Frontiers – Dr. Deb Hamernik, University of Nebraska - Lincoln

Translational Animal Science – Dr. James Oltjen, University of California - Davis

doi: 10.1093/af/vfy040

ASAS Publications

The Journal of Animal Science, an official journal of the American Society of Animal Science, publishes research on animal production and genetics, nutrition, physiology and the utilization of animal products.

Translational Animal Science, an official journal of the American Society of Animal Science, encompasses a broach scope of research topics in animal science, focusing on translating basic science to innovation.

Animal Frontiers, an official journal of the American Society of Animal Science, publishes discussion and position papers that present several international perspectives on the status of a high-impact, global issues in animal agriculture.

To access articles and learn more about ASAS Publications, visit **asas.org**.

2019 ASAS Meetings

Southern Section Meeting
January 26-29 — Oklahoma City, OK

Midwest Section Meeting
March 11-13 — Omaha, NE

Western Section Meeting
June 11-13 — Boise, ID

ASAS-CSAS Annual Meeting
July 8-11 — Austin, TX

Northeast Section Meeting
November 4 — Hershey, PA

News from the Canadian Society of Animal Science

The 2018 joint annual meeting of the American Society of Animal Science and the Canadian Society of Animal Science (ASAS-CSAS) took place in Vancouver, Canada (July 8 to 12) with a strong presence of Canadian scientists, students and professionals. Canadian research was highly represented within the rich scientific content of the meeting in the form of symposia, graduate student competitions and special topics. For the first time, CSAS showcased Canadian content through four symposia (Companion Animal Symposium: Pet Nutrition in Canada, Production, Management and the Environment Symposium: Epigenomics and non-coding RNA regulation of livestock production and health traits, Animal Behavior and Well-Being Symposium: Farm animal welfare management practices and consumer perceptions: Finding a common balance without jeopardizing productivity, and Nutrition, Physiology and Animal Health Symposium: Gut physiology and microbiota influences on animal health and production) and four sessions of graduate student oral competitions. The success of the meeting was ensured by the generous donations by American and Canadian Companies, the hard work put in by the organizing committee and our hard working professionals and students. We extend immense thanks to all these companies and individuals. In particular, Jefo Canada's support at the Diamond level and continuous support from Canadian Science Publishing is highly commendable.

2018 CSAS AWARD RECIPIENTS

The meeting was also a venue where our researchers and students were recognized for their hard work. Students were recognized in the following categories (1) undergraduate achievement ward (8 winners), graduate student travel fellowship (8 winners), graduate student poster competition (3 winners) and graduate student oral competition (6 winners). Support for these student awards was made possible by the Canadian Science Publishing.

A cross section of happy graduate student winners pose for a picture with the President (Dr. Eveline Ibeagha-Awemu, 5th from left) and Editor-in-Chief of the Canadian Journal of Animal Science (Dr. Kees Plazier, 2nd from right)

Professional members were also recognized for their hard work in the following categories: Young Scientist Award (Dr. Chengbo Yang, University of Manitoba), Excellence in Nutrition and Meat Sciences (Dr. Peiqiang Yu, University of Saskatchewan), Technical Innovation in Enhancing Production of Safe and Affordable Food (Dr. Luigi Faucitano, Agriculture and Agri-Food Canada). Animal Industries Award in Extension and Public Service (Dr. Daniel Lefebvre, Valacta Laboratories, Ste-Anne-De-Bellevue), and CSAS Fellowship award (Dr. Tim McAllister, Agriculture and Agri-Food Canada).

2018 CSAS Fellow, Dr Tim McAllister (left), receiving his award from the Past President, Dr Michael Steele

2018-2019 Executive board

During the 2018 Annual Meeting, a new executive board was sworn in to pilot the affairs of the association for one year.

Standing from left to right: Dr. Katie Wood (Eastern Director), Dr. Daniel Columbus (Western Director), Dr. Kate Shoveller (Award's Chair), Dr. Eveline Ibeagha-Awemu (President), Dr. Christine Baes (President-Elect), Dr. Kees Plazier (Editor-in-Chief, CJAS). Kneeling from left to right: Dr. Michael Steel (Past President), Dr. Chengbo Yang (Membership Chair), Dr. Filippo Miglior (Past, Past President), Mr. Clayton Robins (Secretary-Treasurer). Not in the photo are: Dr. Flavio Schenkel (Vice President), Dr. Leslie McKnight (Industry Representative), Dr. Mohsen Jafarikia (Industry Representative) and Dr. Sergio Burgos (Director-at-Large).

Many thanks to our sponsors

Jefo · Canadian Science Publishing · Canadian Pork Council / Conseil canadien du porc · Dairy Farmers of Canada · Chicken Farmers of Canada / Les Producteurs de poulet du Canada · CCA Canadian Cattlemen's Association · Alltech · trouw nutrition, a Nutreco company · Masterfeeds, A Canadian Tradition of Animal Nutrition Solutions

Make a difference. Get involved with CSAS.
Membership benefits at :
https://www.asas.org/CSAS/csas-membership

doi: 10.1093/af/vfy041

EAAP

European Federation of Animal Science

EAAP is the International Federation of Animal Science for Europe and the Mediterranean area.
Join EAAP and become member of the most exciting international animal science network and then have access to many services that are indispensible for every animal scientist worldwide

The 70th Annual Meeting of the European Federation of Animal Science (EAAP) will be held in the historic yet contemporary city of Ghent, Belgium. Note that the very first EAAP meeting was held in Ghent in 1955. Ghent is called "Medieval Manhattan" and is known as one of the most beautiful cities in Europe. It is a great location to celebrate the 70th anniversary of the EAAP meeting! The conference will be organized by ILVO from 26 to 30 August at the International Convention Center (ICC).

The central theme of the 2019 conference is: "Animal farming for a healthy world." This theme indicates on the one hand the important role animal production has within the food chain and on the other hand the societal concerns (on climate, environment, animal welfare, food quality, etc.) the livestock sector has to deal with. Knowledge-based innovation in the livestock sector is needed to take all those concerns into account.

The program will cover the latest findings and views on the developments in animal genetics, health and welfare, nutrition, physiology, livestock farming systems, insects, precision livestock farming, as well as cattle, pig, horse, sheep and goat production.

The Annual Meeting is also a unique occasion to introduce the results of international research groups obtained within different collaboration projects, (e.g., Horizon 2020) update knowledge and acquire new ideas for future collaboration and expand your international network. The EAAP 2019 builds on the success of previous EAAP meetings.

The meeting in Ghent will provide an exciting opportunity for scientists working with a wide range of animal species and disciplines to meet and discuss the latest developments in animal sciences.

We hope that all of you will have a very productive scientific meeting and that you will enjoy the social events and our warm and friendly atmosphere.

Last year in Dubrovnik we had 71 Sessions, 1144 abstracts, 452 Posters and 1178 participants, with 60 countries represented. We hope to achieve the same success this year, if not better. We are looking forward to seeing you in Ghent in August 2019!

For more information concerning this meeting, please contact:
info@eaap2019.be

Conference Information:
http:// www.eaap2019.org

EAAP is also active on Social Media,

Please follow us on Facebook and Twitter
Facebook:
https://www.facebook.com/EAAP.ORG
Twitter: https://twitter.com/eaapofficial

Abstract submission
Information and Guidelines:
www.wageningenacademic.com/eaap
Deadline for submission: March 1, 2019.
Information is available at the congress website: www.eaap2019.org

Scholarship funds for young scientists will also be available.
Please read the instructions:
http://www.eaap2019.org/scholarship
Deadline for submission: March 1, 2019.

doi: 10.1093/af/vfy038

INDIVIDUAL MEMBERSHIP OF EAAP

The EAAP membership is open to all scientists. It is a great opportunity to be up-to-date on the latest publications and other relevant information in the animal sector. We have more than 3,500 current members! It is easy to join, please contact http://www.eaap.org/Content/Individual_Member_Information.html

Membership is free of charge for most European scientists and the membership fee for scientists from non EAAP member countries is very modest.