INTRODUCTION

Thermal stress in hot and humid conditions limits beef cattle production. Over 65% of the world's cattle (beef and dairy) reside in tropical or subtropical climates known for their hot and humid conditions (Burrow, 2012). Reduced animal performance such as lower pregnancy rates, impaired immune function, and reduced feed intake as a result of thermal stress (Amundson et al., 2006; Renaudeau et al., 2012) have a profound economic impact for producers. In the United States alone, thermal stress results in a loss of $369 million a year (St-Pierre et al., 2003). These economic losses are expected to increase as thermal stress increases due to climate change (Hahn, 1999; Renaudeau et al., 2012). There is a strong correlation between production level and metabolic heat production (Renaudeau et al., 2012). In order to maintain an elevated production level in the presence of heat stress cattle must also have a greater capacity for heat loss (O'Brien et al., 2010). Genetic variants identified for increased heat loss can be incorporated into genomic selection programs in order to increase thermotolerance while also maintain high levels of production (Hansen, 2004; Porto-Neto et al., 2014; Garner et al., 2016).

LITERATURE REVIEW

Production and Economic Loss Due to Heat Stress

Production Loss

Reduced animal performance such as lower pregnancy rates, decreased feed intake, and slower growth has a significant economic impact on the beef industry (Amundson et al., 2006; Renaudeau et al., 2012). The U.S. beef industry is greatly segmented and often the challenges that impact these different segments vary greatly (Lowe et al., 2009); however, heat stress negatively impacts each and every segment and results in production and economic losses (St-Pierre et al., 2003). The seedstock and cow calf segments suffer from reduced pregnancy rates (Amundson et al., 2006; Hansen, 2009). Stocker and feedlot operations are particularly impacted by reduced feed intake and growth (Mitlöhner et al., 2001). All of these segments are negatively impacted by decreased immune function (Hahn, 1999; Bernabucci et al., 2010) and the increase of dark cutters negatively impacts the packing segment (Kadim et al., 2004). In 2003 St. Pierre et al. estimated that these losses cost the U.S. beef industry $369 million a year.

Reproduction

High ambient temperature and humidity negatively impact reproduction in beef cattle. Homeokinetic changes to regulate body temperature under heat stress can compromise reproductive function (Hansen, 2009). High THI decreases both male and female fertility, depresses estrus activity, delays puberty in heifers and increases the postpartum interval (Amundson et al., 2006). In males, heat stress can cause an increase in testicular temperature, which results in reduced sperm production, decreased sperm motility and increased morphologically abnormal sperm (Hansen, 2009). The effects of heat stress on female fertility are more complex. Amundson et al. (2006) found the relationship between THI during the breeding season and pregnancy rate in beef cows to be linear. As THI increased, pregnancy rate was found to decrease, with conception rate decreasing by as much as 24% when THI was greater than 72.8 for beef cows on pasture. Several factors contribute to this decrease in pregnancy rate. Feed intake is often reduced under heat stress conditions, altering energy balance, which can reduce cyclicity, depress estrus and delay puberty in heifers (Amundson et al., 2006; Hansen, 2009). Heat stress can also compromise both the oocyte and the follicle in which it is encased (Hansen, 2009). If an oocyte is able to develop and become fertilized preimplantation embryos are also highly sensitive to maternal heat stress. Putney et al. (1989) evaluated the effect of summer heat stress on pregnancy rates in dairy cattle and found that embryos were sensitive to maternal heat stress in the first 7 days after estrus and that embryo transfer after this critical period may alleviate heat stress induced infertility. However, heat stress has also been demonstrated to prolong the postpartum period, with cattle exposed to heat stress during pregnancy taking a longer time and more services to rebreed compared to cattle that did not experience heat stress during pregnancy (Jordan, 2003).

Immune function and metabolism

Short term changes in immune function are often necessary to survive acute heat stress, such as a heatwave (Renaudeau et al., 2012). White blood cells counts have been reported to be markedly reduced by heat stress and to remain low for several days after exposure to heat stress (Hahn, 1999). The ability of bovine monocytes and leukocytes to proliferate is reduced under high temperatures, which may depress cell-mediated immunity (Bernabucci et al., 2010). Greater instances of mastitis in dairy cattle have also been reported during heat stress, which may be a result of decreased immune function under high temperatures (Renaudeau et al., 2012). Heat-induced increase in circulating cortisol may cause a shift from T helper 1 cellular immunity to T helper 2 humoral immunity, increasing infection susceptibility (Bernabucci et al., 2010). Heat stress has also been reported to cause oxidative stress and alter metabolism (Hahn, 1999; Bernabucci et al., 2010). Acute heat stress alters the status of the pituitary as well as the pituitary-thyroid-peripheral tissue axis (Kahl et al., 2015). Exposure to heat stress results in decreased plasma concentrations of thyrotropin, thyroxine, and glucose and increased plasm insulin concentrations (O’Brien et al., 2010; Kahl et al., 2015). These changes cannot simply be attributed to decreased dry matter intake due to heat stress as both studies restricted the dry matter intake of the non-heat stressed animals (O’Brien et al., 2010; Kahl et al., 2015). The changes in metabolism as a result of heat stress exposure are presumably adaptive mechanisms to regulate body temperature (O’Brien et al., 2010)

Feed intake, growth and carcass characteristics

In order to regulate body temperature and reduce heat production, cattle often reduce feed intake when exposed to heat stress (Bernabucci et al., 2010). Hahn (1997) reported that during periods of elevated temperature, cattle ate more frequent meals of smaller size and that total feed intake was reduced, resulting in a major reduction in growth. In addition to decrease feed intake, nutrients are also diverted away from growth towards mechanisms for maintaining body temperature (O’Brien et al., 2010). Heat stress not only limits growth and the quantity of beef production but it negatively impacts beef quality as well. In addition to reduced average daily gain and lighter carcass weights, Mitlöhner et al. (2001) reported the cattle exposed to heat stress without amelioration such as shade or sprinklers also had less subcutaneous fat deposition. Cattle harvested during the summer have also been reported to have increased muscle pH, tougher meat, and a greater incidence of dark cutters than cattle harvested in cooler months, likely due to the physiological stress of heat stress (Kadim et al., 2004).

Economic Impact

The deleterious effects of heat stress result in widespread economic losses for producers. In 2003 St. Pierre et al. estimated that as a whole the U.S. beef industry loses $369 million a year due to lost production due to heat stress. In extreme cases such as summer heat waves these losses can rise dramatically. In 1995 a summer heat wave in the mid central United States caused a loss of $28 million due to animal and performance loss (Hahn, 1999). These estimates likely underestimate the economic losses that the beef industry is currently experiencing as the value of cattle has risen substantially since the estimated were made (Schulz, 2020).

Thermotolerance Adaptations

Hair Adaptations

Hair coat is a key thermoregulatory adaptation that impacts all four major heat loss mechanisms: radiative, conductive, convective and evaporative cooling. Coat color affects the absorption of solar radiation (Bonsma, 1949). Animals with darker coat colors absorb more solar radiation than animals with lighter coat colors (Finch et al., 1984). Cattle with lighter coat colors are able to reflect, rather than absorb, solar radiation, allowing them to stay cooler (Schleger, 1962; Hutchinson and Brown, 1969; Finch et al., 1984). Coat characteristics also affect radiative cooling. Short, sleek hair coats reflect a greater proportion of solar radiation than dense wooly hair coats which can trap solar radiation against the body (Hansen, 2004). Coat characteristics have a similar impact on conductive and convective cooling as well. Short, slick hair coats facilitate conductive and convective heat flow while thick, dense hair coats reduce heat loss through conduction and convection by insulating the animal and preventing contact with cooling surfaces, water or air (Berry and Shanklin, 1967; Finch, 1985; Hansen, 2004).

Skin Adaptations

Skin properties are an important adaptation of thermotolerant breeds. Thermotolerant *Bos indicus* cattle have less resistance to heat flow from the core of the body to the skin than heat sensitive *Bos taurus* cattle (Finch, 1985). The general structure of the skin is the same between breeds of cattle however the shape and size of the different skin components have been found to vary between thermotolerant and non-thermotolerant breeds (McEwan Jenkinson and Nay, 1973). Cattle have been shown to have apocrine sweat glands (Findlay and Jenkinson, 1960) with a general skin structure consisting of: an epidermis, dermis and each hair follicle associated with an arrector pili muscle, sweat gland and sebaceous gland (McEwan Jenkinson and Nay, 1973). *Bos indicus* cattle have been reported to have larger sweat glands that are closer to the surface of the skin (Ferguson and Dowling, 1955) as well as a higher density of sweat glands (Nay and Hayman, 1955). The epithelial layer of these sweat glands has also been shown to have more layers of cells (Carvalho et al., 1995) and the epithelial layer is thought to play in important functional role in the secretion of sweat from the glands (Amakiri and Adepoju, 1979). Nay and Hayman (1955) also reported that the structure of the sweat glands differed between indicine and taurine breeds, with indicine cattle having longer, sac-like sweat glands with few convolutions while taurine cattle had more convoluted sweat glands with a smaller diameter. McEwan Jenkinson and Nay (1972) also reported that zebu cattle had sac-like sweat glands compared to many taurine breeds. Cattle with a greater sweat gland diameter and deeper hair follicles have been reported to be more adapted to hot climates (McEwan Jenkinson and Nay, 1973). *Bos indicus* cattle have also been reported to have a greater hair follicle density (Ferguson and Dowling, 1955). The relationship between skin morphology and sweating rate remains uncertain as sweating rate in unadapted *Bos taurus* breeds has been shown to be higher than *Bos indicus* breeds under heat stress, which may be a result of more effective heat loss through other mechanisms by *Bos indicus* cattle rather than a superior sweating ability of *Bos taurus* breeds (Hansen, 2004).

Relationship between Hair and Skin Adaptations

Hair length and hair coat density impact the effectiveness of evaporative heat loss (Turner and Schleger, 1960; Collier et al., 2008). Cattle with long hair or wooly coats will trap sweat against the hair skin-interface, preventing the sweat from evaporating and cooling the body (Olson et al., 2003). The relationship between hair and skin traits runs much deeper, however. Cattle have apocrine sweat glands, with one sweat gland associated with each hair fiber. Thus, hair density also directly affects the number of sweat glands an animal has (Collier et al., 2008). Mutations that impact hair length have been reported to impact skin characteristics as well.

Senepol cattle that exhibit the slick phenotype are described as not only having a shorter hair coat but also as having fewer hair follicles and larger sweat glands (Huson et al., 2014).

Genetic Regulation of Thermotolerance Adaptations

Genetic Regulation of Hair Adaptations

Differences within and between breeds exist for hair coat properties, indicative of opportunities for selection (Landaeta-Hernández et al., 2011; Hamblen et al., 2018). Several nongenetic factors also regulate hair coat, including seasonal variation, age, sex and nutritional status (Turner and Schleger, 1960). Nevertheless, hair characteristics have been reported to be moderate to highly heritable as shown in Table 1.

Table 1. Heritability estimates of hair characteristics.

Hair Characteristic	Heritability Estimate	Publication
Hair follicle length	0.55±0.27	(Jenkinson et al., 1975)
Hair follicle depth	0.69±0.24	(Jenkinson et al., 1975)
Coat score	0.27±0.04	(Riley et al., 2012)
Coat score	0.41	(Porto-Neto et al., 2014)
Coat score	0.63	(Turner and Schleger, 1960)
Hair thickness	0.16	(Abaker Bertipaglia et al., 2007)
Hair length	0.18	(Abaker Bertipaglia et al., 2007)
Hair diameter	0.12±0.07	(Abaker Bertipaglia et al., 2007)

Contrary to the general expectation that quantitative traits are controlled by a large number of genes, each with a small effect, there have been reports of genes with large effects on hair characteristics (T. A. Olson et al., 2003; Littlejohn et al., 2014; Laercio R Porto-Neto et al., 2018). Evidence of a major gene affecting hair length was first reported by T.A. Olson and colleagues in 2003 (T. A. Olson et al., 2003). The causal mutation was eventually mapped to *prolactin receptor* (*PRLR*) on BTA 20 (Littlejohn et al., 2014). This mutation, known as *slick* is a single base deletion (GC > G) in exon 10 of *PRLR* that introduces a premature stop codon, which disrupts the C-terminal disulphide bridge and results in a truncated receptor (Littlejohn et al., 2014). Two other truncation mutations in *PRLR* that result in a shorter hair coat have also been identified in two more Criollo breeds, Limonero and Carora (Porto-Neto et al., 2018). These truncation mutations are believed to result in a shorter cytoplasmic domain in the receptor, disrupting the *Jak2/Stat5* signaling pathway (Porto-Neto et al., 2018). A reciprocal mutation has also been identified in *prolactin (PRL)* (Littlejohn et al., 2014). A nonsynonymous SNP in exon 5 of *PRL* (A>C) is believed to be the causal mutation for the *hairy* mutation, which results in cattle with long, hairy coats and poor lactation and thermoregulation (Littlejohn et al., 2014). The prolactin pathway not only regulates hair length but lactation as well (Karg and Schams, 1974; Horseman and Gregerson, 2013; Littlejohn et al., 2014).

Genetic Regulation of Skin Adaptations

Unlike hair adaptations, no major genes impacting skin adaptations have currently been reported. However, several skin characteristics have been reported to moderately to highly heritable as shown in Table 2.

Table 2. Heritability estimates of skin characteristics

Skin Characteristic	Heritability Estimate	Publication
Sweat gland length	0.76±0.20	(Jenkinson et al., 1975)
Sweat gland diameter	0.58±0.23	(Jenkinson et al., 1975)
Sweat gland volume	0.74±0.26	(Jenkinson et al., 1975)
Sweating rate	0.10±0.07	(Abaker Bertipaglia et al., 2007)

Major differences in skin characteristics between breeds and breed groups have also been reported, indicative of opportunities for selection (Jenkinson and Nay, 1973; Jenkinson et al., 1975; Carvalho et al., 1995). Jenkinson and Nay (1973) reported that in general Asian, African and South American cattle tended to have smaller sweat gland volumes closer to the skin's surface than European cattle although there was variation in sweat gland morphology in some European breeds. Carvahlo et al. (1995) reported that native *Bos indicus* cattle had a greater rectal temperature, greater sweat gland perimeter and a greater number of epithelial strata than Simmental cattle. Sweating rate has also been reported to be higher in thermotolerant *Bos indicus* cattle then *Bos taurus* cattle (Finch, 1985).

Selection for Thermotolerant Animals

Selection for genetic variants associated with increased heat loss may be a solution to increase thermotolerance while also maintain high levels of production (Hansen, 2004; Porto-Neto et al., 2014; Garner et al., 2016). Body temperature under heat stress has been shown to be moderately heritable (Dikmen et al., 2012; Riley et al., 2012; Porto-Neto et al., 2014). However, selection for lower body temperature alone without regard to heat loss mechanisms may result in a decrease in production by selecting for animals with lower heat production as a result of lower feed intake or basal metabolism (Bonsma, 1949; Hansen, 2004). In order to maintain an elevated production level in the presence of heat stress cattle must rather have a greater capacity for heat loss (O'Brien et al., 2010)

Coat color and characteristics can be used to select for more thermotolerant animals as these traits have a large impact on an animal's ability for heat loss (Bonsma, 1949; Finch, 1985). Both coat color and score (a qualitative evaluation of coat characteristics) have been found to be correlated to an animal's body temperature (Porto-Neto et al., 2014). Coat color can be selected for in a very straightforward manner as it is a qualitative rather than quantitative trait under the control of a very small number of major genes (Schmutz, 2012). However, despite the thermotolerant advantage of lighter coats, the National Beef Quality Audit reported that 57.8% of the cattle harvested in the U.S. in 2016 were black or predominately black hided (Eastwood et al., 2017). The prevalence of black hided cattle is likely due to economic incentives. Cattle that qualify for branded beef programs often receive premiums and one of the first qualifications for many of these programs is hide or coat color, such as Certified Angus Beef which requires cattle to be 51% blackhided, in addition to carcass specifications (USDA, 2011). Black hided calves receive a high price /cwt because of the potential for acceptance in the Certified Angus Beef program as well as perceived differences in performance potential (Mccabe, 2018). Selection on hair coat characteristics rather than color may be more practical under current U.S. beef industry constraints. The *slick* mutation in the gene *prolactin receptor (PRLR)* has already been identified in Senepol cattle (Olson et al., 2003; Littlejohn et al., 2014). This mutation has a major impact on hair length and is an excellent candidate for selection for a shorter, slicker hair coat in cattle. However, mutations in *PRLR* have only been identified in Senepol and other Criollo breeds of cattle (Laercio R. Porto-Neto et al., 2018) which are not prevalent in the United States.

Additionally, *PRLR* plays an important role in lactation (Karg and Schams, 1974) and it is currently not well understood what impact the currently identified mutations would have on lactation and subsequently calf weaning weight.

CONCLUSIONS AND IMPLICATIONS TO GENETIC IMPROVEMENT OF BEEF CATTLE

Substantial differences for thermotolerance exist within and between breeds, indicative of opportunities for improvement through selection. However, thermotolerance may have an antagonistic relationship with some production traits. Increased production such as faster growth and greater lactation may also result in an increase in heat production. Selecting for animals with an increased ability for heat loss may allow animals to maintain high levels of production while increasing thermotolerance. However, many traits that contribute to heat loss, such as hair and skin characteristics, can be difficult and expensive to measure, indicating that genomic selection may be more useful than traditional. The traits are also excellent candidates for genomic selection, as contrary to the general expectation that a large number of genes have a small effect, previous studies have reported genes with large effects on these traits. Causal variants identified for these traits can be used to increase the accuracy of genomic selection and can also be utilized across populations and breeds. Additionally, these variants can be used to determine biological pathways for correlated traits.

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