Invited review: Influence of climatic conditions on the development, performance, and health of calves

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ABSTRACT

The objective of this review is to provide the reader with an overview of thermoregulatory mechanisms and the influence of climatic conditions in different housing systems on the development, performance, and health of calves. Thermic stress is observed in association with extreme temperatures and large temperature variations, but other variables such as relative humidity and wind speed can also contribute to thermic stress. Thermoregulation in calves is similar to that in adult cattle, but especially dystocical calves are more prone to heat loss. Heat or cold stress results in direct economic losses because of increased calf mortality and morbidity, as well as indirect costs caused by reduced weight gain, performance, and long-term survival. The climatic conditions in a variety of housing systems, associated health problems, and strategies to mitigate thermic stress are discussed in this review. The goal of housing is to alleviate the effect of climate on calves and provide a microclimate. Adequate ventilation with fresh air is essential to reduce respiratory disease. Common practices such as raising calves in individual outdoor enclosures have been challenged lately. Recent research seeks to evaluate the suitability of group housing under practical, economic, and animal welfare considerations. Limited results for reducing thermic stress can be achieved by simple measures such as shades or shelter, but additional heat or cold stress relieving strategies can be required depending on the housing system.

Key words: calf, climate, thermoregulation, heat stress, cold stress

INTRODUCTION

Thermoregulation is the ability of homeothermic animals to keep their body temperature within a certain range despite being exposed to different ambient temperatures (Bligh, 1998). A physiological core tem-

perature is maintained by generating metabolic heat as well as exchanging heat with the environment (Da Silva, 2012).

Animals are able to adjust to adverse climate by means of acclimatization and adaptation (Roy and Collier, 2012). Extreme climatic conditions that cannot be compensated by thermoregulatory mechanisms result in thermic stress. Thermic stress in calves has a negative effect on animal welfare (Silanikove, 2000) and causes direct economic losses in the form of mortality and morbidity, and indirect costs caused by reduced weight gain, performance, and long-term survival (Virtala et al., 1996; Donovan et al., 1998; Snowden et al., 2006). Because some subspecies and breeds are better adapted to a hot climate (Cartwright, 1955; Silva et al., 2013), efforts have been made to create heat-resistant and high-performing crossbreeds, but with varying results (McDowell, 1985; Rutledge, 2001; Eberhardt et al., 2009).

Different housing systems have been developed to protect calves from extreme climatic conditions and thermic stress. Depending on the climate, culture, and intended use of animals (e.g., beef versus dairy) these include open range, shelters, pens, or hutches, and naturally or mechanically ventilated stables (Seedorf et al., 1998; Moran, 2002; Marcé et al., 2010). Whereas some housing systems principally succeed in providing thermal comfort to calves, other problems, such as poor air quality, might arise from their use. Ongoing research aims to identify the best housing system for a particular climate.

Diarrhea and respiratory disease, the 2 most common health problems when raising calves, are typically caused by multiple factors, with climate and housing system playing an important role in the etiology (Roy, 1980; Barrington et al., 2002; Gorden and Plummer, 2010; Walker et al., 2012). The incidence of respiratory diseases tends to be higher in calves reared in mechanically ventilated barns than in calves housed with natural ventilation or in outdoor enclosures (Okamoto et al., 1993; Wójcik et al., 2012; Table 1).

Many publications cover specific aspects of thermoregulation, thermic stress, effect of climatic conditions

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Table 1. Selected studies analyzing the influence of housing type on calf performance¹

Study	Animals	Season	Region	Duration	Treatment	Control	Weight gain	Feed intake	Respiratory disease incidence	Diarrhea incidence
Davis et al. (1954)	32 newborn Jersey or crossbred calves	Winter	Washington, US	2 yr; up to 6 mo/calf	Outdoor individual pen	Closed barn	Pos	NA	Neg	Neg
Hanekamp et al. (1994)	13 batches of 80 red-and-white bull calves	All seasons	Netherlands	5 yr; 6 mo/calf	Open barn	Closed barn	—	—	—	NA
Hepola et al. (2006)	80 male Friesian and Ayrshire calves	All seasons	Finland	5 yr; 12 wk/calf	Outdoor group housing	Indoors (cow barn)	Neg	—	NA	NA
Jorgenson et al. (1970)	60 Holstein calves	All seasons	North Dakota, US	26 wk/calf	Outdoor hutches/open sheds	Heated barn	—	—	—	—
McKnight (1978)	68 newborn male Holstein calves	All seasons	Ontario, Canada	3 yr; 49 d/calf	Outdoor movable pen	Stall in enclosed barn	—	Pos	—	Neg
Murley and Culvahouse (1958)	122 female calves	All seasons	North Carolina, US	4 yr; 16 wk/calf	(a) open shed; (b) portable pen	Conventional barn	—	—	Neg	—
Nilsson (2012)	793 heifer calves	All seasons	Sweden	4 yr	Outdoor group hutches	Naturally ventilated barn	NA	NA	Neg	Neg
Okamoto et al. (1993)	9 male Holstein calves	Winter	Japan	3 winters	Outdoor hutch	Heated stable	—	—	Neg	—
Richard et al. (1988)	42 Holstein calves	Fall to spring	Pennsylvania, US	NA	Outdoor individual hutches	Mechanically ventilated barn	Pos	—	Neg	NA
Wójcik et al. (2012)	90 Holstein bull calves	Summer/fall	Germany	84 d	Group igloo hutches	Calf barn (group pens)	Pos	Pos	Neg	NA

¹Pos = treatment has a positive effect on parameter compared with control. Neg = treatment has a negative effect on parameter compared with control. — = treatment has no effect on parameter compared with control. NA = not analyzed in this study.

and housing conditions, as well as husbandry-associated diseases in calves. Although several reviews have been published on the effect of climate and thermic stress on cattle and dairy cows, to our knowledge this is the first comprehensive review covering the influence of climatic conditions and housing system on the performance and health status with a focus on calves.

THERMOREGULATION

Homeothermic animals keep their body temperature almost constant. They generate metabolic heat and continuously exchange heat with the environment. The rate of heat exchange depends on the climatic environment and the thermoregulation mechanisms of an animal. Thermoregulation involves physiological, morphological, and behavioral mechanisms (Khalifa, 2003; Ivanov, 2006; Da Silva, 2012). The heat balance of an animal is composed of the heat produced by metabolic and muscular activity as well as heat exchanges with the environment (IUPS, 2001). The mechanisms of heat transfer (convection, conduction, thermal radiation, and evaporation) are well known and explained, for example, by Turnpenny et al. (2000) and Spiers (2012).

Calves are born with functional thermoregulatory mechanisms (Gluckman et al., 1999; Schäffer and von Borrell, 2008). Approximately 2% of their BW is composed of brown adipose tissue, which is involved in nonshivering thermogenesis (Alexander et al., 1975; Morrison, 2004). Intake of colostrum also contributes to heat generation (Vermorel et al., 1989b). Newborn calves, however, are prone to heat loss under cold conditions because of their low surface/mass-ratio and poor insulation [i.e., thin skin and subcutaneous fat (Gonzalez-Jimenez and Blaxter, 1962; Olson et al., 1980a; Berman, 2003; Van Iaer et al., 2014)]. Further, they cannot rely on heat production by ruminal fermentation (Collier et al., 1982). Healthy calves are physically active, which increases heat production and cold resistance (Vermorel et al., 1989b). They are remarkably tolerant toward sustained cold if hair coat and bedding are dry, the lying area is protected from drafts, and sufficient nutritional energy is provided (Rawson et al., 1989b; Schäffer and von Borrell, 2008; Nonnecke et al., 2009). In dystocial calves, heat generation mechanisms are often impaired. Inhibited vasoconstriction and muscle shivering, and reduced activity result in a lower tolerance toward cold. Thermogenesis in dystocial calves is up to 36% lower than in eutocial calves (Vermorel et al., 1989a). Thus, diseased or weak calves should be housed in a warm and dry environment (Martin et al., 1975). Under cold conditions, infrared lamps can be used to provide a warm microclimate. Borderas et al. (2009) installed infrared heat lamps in calf pens in a

naturally ventilated barn during winter and studied the temperature preferences of newborn dairy calves. The calves spent more time under the heat lamps than in other pen areas. The heat lamps were sought after by the older calves more often, indicating a better ability to thermoregulate by actively choosing warm places with increasing age.

Body temperature and heat production of mammals typically follow a circadian rhythm and vary with activity, resulting in changing thermal requirements during the day (Berman and Zamsky, 1971; Schrama et al., 1994). In newborn calves, the rhythmicity of body temperature is absent during the first week after birth, but develops and stabilizes during the first 2 mo of life (Piccione et al., 2003). The physiological range of the rectal temperature of calves is 38.1 to 39.2°C (Moran, 2002; Piccione et al., 2003). In an Italian study, the mean rectal temperature of calves with an established temperature rhythm exposed to natural summer temperatures (22 to 28°C) was 38.3°C, with diurnal variations of 1.4°C. In 2-mo-old calves, body temperature increased during the day, peaked in the evening, and decreased during the night (Piccione et al., 2003). Rectal temperature was shown to increase with a high ambient temperature and decrease with high relative humidity and wind velocity. This should be taken into consideration when using it as a diagnostic tool (Theurer et al., 2014).

Little information is available with regard to differences in thermoregulation under hot conditions between calves and adult cattle. Klemm and Robinson (1955) showed that evaporating heat loss increased with age from 1 to 8 mo in Australian Illawara Shorthorn calves. Broucek et al. (2009) evaluated the effect of hot temperatures on performance and on the hemogram of Holstein calves and concluded that the calves were able to maintain homeostasis under prolonged heat stress.

The existing knowledge of many basic principles of thermoregulation is often based on experiments with other species. More studies are warranted to confirm that the results are fully applicable to bovines under current management conditions. Studies concerning the thermoregulation of the bovine fetus are also limited.

Some studies dealing with thermoregulation or thermal stress (Klemm and Robinson, 1955; Berman and Zamsky, 1971; Christison and Johnson, 1972; King et al., 2006; Bertagnon et al., 2011) are based on a small number of animals. Other studies cover a specific climatic region only (Ehrenreich and Bjugstad, 1966; Frank and Kaneene, 1993; Donovan et al., 1998; Svensson et al., 2003; Broucek et al., 2008; Gulliksen et al., 2009b) or are based on observations from a single herd, farm, or research station (Hoshiba, 1986; Diesch et al., 2004a,b; Wójcik et al., 2012).

Thermoneutral Zone and Critical Temperatures

The thermoneutral zone (**TNZ**) is the range of ambient temperatures in which the heat production of an individual is independent from the environmental temperature (Webster, 1974; Spiers, 2012). The TNZ is comfortable for the animal, the core temperature is generally within physiological limits, and body temperature regulation is achieved only by sensible heat loss (Charles, 1994; IUPS, 2001). Some researchers divide the TNZ into subzones [e.g., the zone of thermal wellbeing and zones in which moderate activation of thermoregulatory mechanisms occurs (Silanikove, 2000)]. If the ambient temperature falls below the lower critical temperature (T_{lc}), the rate of metabolic heat production increases to maintain thermal balance. If the ambient temperature exceeds the upper critical temperature (T_{uc}), heat is dissipated via sensible heat loss and evaporation (IUPS, 2001). If the thermal strain on the animal is too high and body temperature continues to rise (or fall) despite activation of all possible thermoregulatory mechanisms, hyperthermia (or hypothermia) occurs (Silanikove, 2000). For most mammals, a core temperature exceeding 45°C is fatal, resulting in brain damage. A core temperature of below 27°C can cause lethal cardiac fibrillation (Robinson, 2013). Robinson and Young (1988) demonstrated that calves can recover from a rectal temperature as low as 30°C.

The TNZ depends on various physiological and environmental factors [e.g., age, size, breed, nutrition, hair coat, behavior, bedding, and weather (Webster, 1974; Holmes et al., 1978; Schrama et al., 1993b)]. Thus, a variety of TNZ for calves can be found in the literature, ranging from 0 to 26°C (Wathes et al., 1983; Nonnecke et al., 2009). Reported T_{lc} values range from 0 to 18°C, depending on the age of the calves. Wet and windy weather conditions result in an increase of T_{lc} (Gonzalez-Jimenez and Blaxter, 1962; Webster et al., 1970; Webster, 1974; Schrama et al., 1993a,b). With regard to T_{uc} , less information is available. Spain and Spiers (1996) indicated a T_{uc} of 26°C, above which calves exhibit an increased respiratory rate.

Role of the Nervous System in Thermoregulation

Thermoreceptors are sensory neurons (type A δ or C) in the skin, brain, and viscera that respond to heat or cold (Nagashima et al., 2000; Schepers and Ringkamp, 2010). Different types of temperature-activated transient receptor potential ion channels have been identified in cutaneous sensory neurons and skin cells, and seem to respond to different temperature ranges (Bandell et al., 2007; Lumpkin and Caterina, 2007;

Schepers and Ringkamp, 2010). The traditional school of thought states that afferent signals are passed via the spinal dorsal horn and the lateral parabrachial nucleus to the preoptic region of the hypothalamus, where they are compared with the thermal status of the hypothalamus itself (Morrison and Nakamura, 2011; Robinson, 2013). If a deviation is detected, effectors (such as vasculature muscle cells, skeletal muscle cells, or brown adipocytes) are activated by parallel effector-specific core-efferent pathways. This results either in producing or dissipating heat, for example by vasoconstriction or vasodilation, muscle shivering, or the activation of brown adipose tissue (Nagashima et al., 2000; Morrison, 2004; Morrison and Nakamura, 2011; Robinson, 2013). Another ascending route is the spinothalamocortical pathway, which mediates conscious thermal reception (Craig et al., 1994). A detailed review of neural pathways for thermoregulation is provided by Morrison and Nakamura (2011) and Nagashima et al. (2000). The theory of a comparison of input from thermoreceptors with a single central set point temperature has been challenged lately. The function of peripheral receptors as “comparators” without the transmission of signals to the brain and the presence of independent thermoeffector loops for body temperature regulation have been proposed instead (Kobayashi et al., 2006; Romanovsky, 2007; Werner, 2010). More research is necessary to fully understand the neural pathways of thermoregulation.

Role of the Endocrine System in Thermoregulation

Hormones involved in thermoregulation include predominantly glucocorticosteroids, thyroid hormones, and catecholamines. Glucocorticosteroids, mainly cortisol, are released via the hypothalamic-pituitary-adrenal axis in response to acute (thermal) stress, which results in increased blood glucose availability (Olson et al., 1981; Collier et al., 2006). The concentration of plasma cortisol in calves is typically high at birth and decreases during the first week of life (Hadorn et al., 1997; Hammon and Blum, 1998). It remains high in case of feed deprivation and decreases after feed intake (Lee et al., 1995; Hammon and Blum, 1998). Plasma cortisol levels sharply increase 20 min after the beginning of acute moderate thermal stress, and reach a plateau after 2 to 4 h. With chronic, mild heat stress, cortisol levels return to normal after 1 to 2 d, and become depressed with continuous onset of heat stress over several weeks (Christison and Johnson, 1972).

The plasma concentration of triiodothyronine (**T3**) and thyroxine (**T4**) was shown to be high in newborn calves and declined during the first week of life (Ha-

dorn et al., 1997; Egli and Blum, 1998). Grongnet et al. (1985) observed that the T4 profile depended on the diet of calves, whereas other researchers were not able to confirm this observation (Hammon and Blum, 1998). The plasma levels of T3 and T4 decline under warm conditions and increase under cold conditions. They respond slower to external stimuli than glucocorticosteroids (Young, 1981; Khalifa, 2003).

The plasma concentration of the catecholamines epinephrine and norepinephrine is elevated during the perinatal period (Richet et al., 1985; Hammon et al., 2012). Catecholamines are released during acute thermal stress and act together with an increased sympathetic activity (Olson et al., 1981; Young, 1981). An increased level of antidiuretic hormone has been found during heat stress, which is linked to the need to conserve water (Beede and Collier, 1986). Further hormones involved in temperature-related metabolic changes include somatotropin, IGF-I, insulin, and prolactin (Roy and Collier, 2012).

Acclimatization, Acclimation, and Adaptation

Acclimatization describes the change in phenotype by which individuals adjust to exposure to several environmental stressors. Acclimation refers to a single stressor. Adaptation describes the permanent change in the genotype of a population in response to environmental conditions (Roy and Collier, 2012).

Acclimatization includes endocrine, cellular, and metabolic responses. Examples for seasonal acclimatization include hair coat thickness, fat deposition, or increased feed intake (Roy and Collier, 2012). With climatic stress, acclimatization takes days or weeks and is fully achieved when the body temperature returns to the prestress level (Nienaber et al., 1999). On the endocrine level, a decrease in thyroid hormone levels occurs in response to heat acclimatization (Silanikove, 2000). Metabolic rate and heat production increase with cold climate and decrease with warm climate (Young, 1981; Brown-Brandl et al., 2003). Water and electrolyte metabolism, however, is accelerated with chronic heat stress (Beede and Collier, 1986).

A short-term and a long-term phase of acclimatization can be distinguished. Short-term acclimatization involves behavioral mechanisms, activation of the nervous and endocrine system, and changes in cellular signaling pathways. During long-term acclimatization, a change in gene expression takes place and the effect of the stressors on the animal is reduced (Collier et al., 2006; Roy and Collier, 2012). Hahn et al. (1990) observed that cattle cope with heat via behavioral mechanisms (e.g., reduction of feed intake), followed

by physiological mechanisms after 2 to 4 d of exposure. Brown-Brandl et al. (2003) studied acclimatization in feeder cattle and found that a metabolic shift occurred between acute and chronic heat stress. The respiration quotient (liters of carbon dioxide produced divided by liters of oxygen consumed) increased and heat production decreased with acclimatization to heat stress. Sudden heat waves affected nonacclimatized animals more severely (Brown-Brandl et al., 2005). Critical temperatures and the TNZ change during acclimatization. Animals kept permanently under cold climatic conditions exhibited an increased basal metabolic rate and a reduced upper and lower critical temperature (Webster et al., 1970; Young, 1983; Robinson et al., 1986). Acquired heat tolerance might be linked to increased levels of heat shock protein (Kregel, 2002).

Certain subspecies and breeds are better adapted to certain climatic conditions than others; for example, *Bos indicus* (Zebu) cattle are better adapted to tropical climates, whereas *Bos taurus* cattle are better adapted to temperate climates (Finch, 1986; Eberhardt et al., 2009; Silva et al., 2013). Factors that likely contribute to the higher heat tolerance of Zebu breeds include a lower metabolic rate, lower resistance in the heat transfer from tissues to skin, different sweating patterns, more arteriovenous anastomoses, and different coat types (Finch, 1986; Roy and Collier, 2012). Thus, it can be more profitable and sustainable to use indigenous breeds or crossbreds in tropical regions (Cartwright, 1955; King et al., 2006). On the other hand, Brahman calves have more difficulties adapting to cold environments compared with crossbred calves. In a study by Godfrey et al. (1991), Brahman calves had lower rectal temperatures and were less able than crossbreds to use energy-containing blood constituents (glucose, triglyceride, nonesterified fatty acids, and so on) to increase their body temperature when exposed to a cold environment (4°C).

For a long time, efforts have been made to produce a heat-tolerant yet high-producing breed by crossbreeding dairy breeds and tropical breeds. First-generation offspring (F₁) sired by dairy breeds tend to perform better than other crosses or indigenous cattle under extensive conditions (McDowell, 1985; McDowell et al., 1996; Rutledge, 2001). Klemm and Robinson (1955) demonstrated that young Zebu-Hereford crosses exhibited a higher heat tolerance due to a superior sweating mechanism and decreased heat production compared with Jersey or Illawarra Shorthorn calves. Other crosses besides the F₁ have not succeeded so far because favorable epistatic combinations tend to be lost during recombination at meiosis (Syrstad, 1989; Rutledge, 2001).

THERMIC STRESS

Thermic stress can be defined as a change in the thermal environment, which causes a change in body temperature that is not compensated by thermoregulatory mechanisms. The deviation of the body temperature and activation of thermoregulatory effector organs caused by thermic stress is defined as thermic strain (IUPS, 2001). Both terms are often used interchangeably (Spiers, 2012). Uncompensated thermic strain on calves can lead to hyper- or hypothermia, and in extreme cases to heat stroke, frostbite injuries, or death (Martin et al., 1975; Olson et al., 1980a; Cruz and Naylor, 1993). Although temperature is the most widely used measure to assess thermal stress, other parameters can influence the perception of warmth or cold of an individual. For example, high humidity or solar radiation amplifies the effect of high temperatures, whereas high wind velocity or precipitation increases the perception of low temperatures (Da Silva, 2012). Precipitation has a negative effect on calf survival, especially when combined with low temperatures (Azzam et al., 1993; Stull et al., 2008). Climatic measurements to evaluate thermic stress should ideally be taken directly on the farm as these measurements often deviate from official meteorological data (Schüller et al., 2013).

Cold Stress and Heat Generation

Thermoregulatory responses for heat generation include shivering and nonshivering thermogenesis. Nonshivering heat production mechanisms include an increase of the metabolic rate, piloerection, and vasoconstriction (Robinson and Young, 1988; Rawson et al., 1989a; Ivanov, 2006; Kirch et al., 2008). Piloerection results in an almost doubled depth of the hair coat (Gonzalez-Jimenez and Blaxter, 1962). Newborn calves also generate heat by the oxidation of brown adipose tissue (Alexander et al., 1975; Young, 1981). Behavioral responses to cold ambient temperatures include seeking shelter, increased locomotion, posture, and crowding or huddling (Khalifa, 2003; Da Silva, 2012; Spiers, 2012).

After birth, calves exhibit an initial decrease in body temperature caused by evaporation from the wet hair coat, followed by an increase in body temperature after the coat has dried (Vermorel et al., 1989b; Diesch et al., 2004a). Diesch et al. (2004a,b) studied the physiological status of newborn dairy calves in New Zealand and found that calves born during cold ($<10^{\circ}\text{C}$), wet, and windy weather conditions had lower rectal temperatures and took a longer time to stand up than calves born during warm and dry weather. Rawson et al. (1989b) observed that cold housing conditions (-8 to -30°C) were associated with lower rectal tempera-

tures and respiratory rates and higher heart rates in calves. The metabolic rate of calves exposed to cold was increased, particularly during standing. Scibilia et al. (1987) recorded lower daily weight gains, water intake, rectal temperature, and respiratory rate as well as a 32% increase in maintenance energy requirement for calves raised at -4°C , compared with calves housed at 10°C . In experimentally cold-stressed newborn calves, overall depression, muscle shivering, and relaxation as well as delayed absorption of colostral immunoglobulins were observed (Olson et al., 1980a,b). Robinson and Young (1988) induced hypothermia (rectal temperature of 30°C) in calves by water immersion and evaluated different recovery methods. Peak metabolism during the cooling procedure occurred on average at a rectal temperature of 36°C . Regaining euthermia by placing calves in a warm water bath (38°C) was faster and more efficient than by placing them in a warm box (20 to 25°C) with blankets or infrared heat lamps (Robinson and Young, 1988).

Cold stress leads to increased feed intake, with a higher amount of feed energy directed toward heat production. There is evidence that the digestive function is suppressed under cold stress. In extreme cold, increased DMI cannot match increased heat production, resulting in a drop in performance. Restrictive feeding has a negative effect on cold tolerance, particularly in young calves, whose body fat reserves become depleted quickly (Young, 1981; Scibilia et al., 1987; NRC, 2001). A limited feeding regimen under cold conditions results in a decreased protein synthesis, especially in skin and muscle cells (Scott et al., 1993). Schingoethe et al. (1986) and the NRC (2001) recommended increasing the quantity of liquid diet or the amount of solids (at least 0.56 kg/d) in the liquid diet of calves during cold weather and providing warm water 2 to 3 times per day to stimulate starter intake. Ad libitum feeding strategies account for these demands. The supplementation of fat in the liquid diet during cold stress increases BW gain during the preweaning period but decreases starter intake and can result in a suboptimal ratio of CP to ME (Jaster et al., 1990; Litherland et al., 2014). Nonnecke et al. (2009) compared the performance of preruminant calves in a warm (average temperature 15°C , average relative humidity 59%) and a cold (average temperature 5°C , average relative humidity 68%) environment. The calves and their surroundings in the cold environment were wetted to augment humidity and cold perception. Calves raised in the cold environment exhibited similar weight gains compared with the calves raised in the warm environment, but consumed more concentrates. Okamoto et al. (1993) observed a higher intake of milk replacer by calves raised in simple outdoor housing systems during winter than calves raised indoors.

Calves spend a large amount of time lying down, which conserves heat and decreases critical temperature. A greater heat production is observed in standing versus lying calves; however, it is usually overcompensated by an increased convective and conductive heat loss (Schrama et al., 1993a; Borderas et al., 2009).

Insulation is provided by the subcutaneous adipose tissue, the skin, the hair coat, and the surrounding air layer (McLean, 1963; Rawson et al., 1989a). Cattle that are kept under cold conditions develop a denser hair coat due to reduced hair shedding than cattle kept in warm temperatures (Webster et al., 1970; Krastev, 2002). A higher amount of thermal radiation is absorbed by animals with dark hair coats than with light-colored hair coats (Mader et al., 2002).

Pathologic cold lesions include subcutaneous edema and hemorrhage as well as intraarticular hemorrhage and synovitis, especially at the limbs (Olson et al., 1980a; Rawson et al., 1989b). In very cold regions, frostbite injuries are observed under field conditions. They are often accompanied by other diseases (Cruz and Naylor, 1993). Gulliksen et al. (2009b) observed that calves born during the winter in Norwegian dairy herds were more likely to die during their first week of life than calves born during the summer.

Cold stress is associated with alterations in hematological and biochemical parameters. Higher total protein, albumin (Scibilia et al., 1987), erythrocyte counts, hemoglobin, and hematocrit (Krastev, 2002) have been found in calves kept in a cold environment. Tzou et al. (1991) identified cold-stressed calves based on changes in bilirubin. Serum phosphate (Krastev, 2002), sodium, and potassium (Coban and Sabuncuoglu, 2005) were decreased under cold conditions in some studies. The effect of cold stress on electrolyte status, however, is controversial, and the results are probably influenced by other factors besides temperature. Plasma glucose concentration decreases under cold husbandry conditions (Scibilia et al., 1987; Nonnecke et al., 2009), but increases in response to sudden cold stress (Olson et al., 1981). Nonnecke et al. (2009) reported an increased concentration of nonesterified fatty acids in calves housed in a cold environment. In contrast, Rawson et al. (1989b) did not find any substantial hematological or biochemical changes in cold-stressed calves.

Heat Stress and Heat Dissipation

Whereas heat stress is a constant concern in subtropical or tropical countries, even in temperate regions summer temperatures frequently exceed the TNZ in cattle (Van Iaer et al., 2014). Neuwirth et al. (1979) observed heat stress in calves with an ambient temperature above 32°C and a relative humidity above

60%. Spain and Spiers (1996) observed an increase in the respiration rate in calves at 26°C. At a rectal temperature beyond 40.5°C, minute volumes increased as well, causing a respiratory acidosis (Findlay, 1957). Brown-Brandl et al. (2003) emphasized the diurnal pattern of respiration rate and rectal temperature, which followed ambient temperature with a time lag of 1.5 to 2 h and 4 to 5 h, respectively. Theurer et al. (2014) evaluated the effect of weather variables on thermoregulation of calves during heat stress. They found a positive relationship between ambient temperature and temperature humidity index and the rectal and nasal submucosal temperature. High relative humidity, wind speed, and barometric pressure resulted in a decrease of rectal and nasal submucosal temperature. Under heat stress, nasal submucosal temperature can exceed 39°C, which might result in an inactivation of temperature-sensitive intranasal vaccines (Theurer et al., 2014).

Behavioral modifications observed during heat stress include seeking shade, changing posture (standing vs. lying), body alignment away from the sun, reducing locomotion during hot times of the day, and bunching to seek shade from other animals (Schrama et al., 1993a; Gaughan et al., 2002; West, 2003). With high ambient temperature, feed intake, grazing time, and weight gain decline, whereas water intake rises (Ehrenreich and Bjugstad, 1966; Broucek et al., 2008). Brosh et al. (1998), Mader et al. (2002), and Mader (2003) observed that heat production in cattle increased after feeding and recommended limiting the amount of feed during hot times of the day. The decline in DMI caused a reduction in metabolic heat generated by digestion, thus helping to maintain thermal balance. Whereas digestibility is slightly enhanced due to a longer retention time of ingesta in the gastrointestinal tract, nutrient absorption is reduced due to a decreased blood flow to the intestines. This results in a reduced intake of nutrients under heat stress (Beede and Collier, 1986). The composition of nutrient requirements may also change because of heat stress. Cattle sweat is high in potassium and urinary excretion of sodium is higher than normal under heat stress, meaning potassium and sodium needs might be increased. Furthermore, vitamin A can be required in higher levels (Beede and Collier, 1986). Further research is needed to evaluate the efficiency of feeding strategies in calves that respond to changes in feed intake and excretion of minerals during periods of heat stress.

Calves appear to be affected by heat stress already during the embryonic period (Silva et al., 2013). Evidence suggest that maternal heat stress during late gestation results in impaired fetal growth and immune function of the neonate (Tao and Dahl, 2013). Lower serum immunoglobulin and higher serum corticosteroids

were found in calves exposed to higher temperatures (Stott et al., 1976; Donovan et al., 1986). Bertagnon et al. (2011) found a higher number of monocytes in the blood and a lower number of alveolar giant macrophages in tracheobronchial lavage fluids of calves at high temperatures (30°C) and low humidity (41%), compared with 2 combinations of lower temperature and higher humidity. This suggests that a hot and dry climate suppresses the respiratory immune response. Broucek et al. (2009) investigated the influence of heat stress on hematologic variables and did not find any substantial effect.

INFLUENCE OF HOUSING ON CALVES

From a performance and welfare perspective, calves should ideally be raised in their TNZ and thermal stress should be minimized (Silanikove, 2000). Housing aims to reduce the effect of climate on animals and can provide a specific microclimate. Calves are raised in a variety of housing systems, including open range, individual pens or hutches, and naturally or mechanically ventilated stables. On the one hand, the choice of a specific housing system depends among other factors on the predominant climate in a region (Webster, 1974). On the other hand, each housing system has its own climatic traits and associated benefits and drawbacks. Together with various other factors such as hygiene, feeding practice, or herd management, the type of housing can play a role as a risk factor in disease transmission (Barrington et al., 2002; Marcé et al., 2010). Because of this close interrelation between climate and housing, housing systems are discussed under a climatic point of view to understand their effect on calves' thermal wellbeing. An overview of selected studies comparing the effect of housing type on calf performance and health is provided in Table 1.

According to surveys conducted in Europe, dairy calves are predominantly housed individually in pens (with possible contact to other calves) or hutches (generally outdoors without direct contact to other calves) during the first 2 to 14 wk of life (Marcé et al., 2010; Klein-Jöbstl et al., 2014). In the United States, 68% (Walker et al., 2012), and in Canada, 88% (Vasseur et al., 2010) of preweaned dairy calves are kept in individual pens or hutches.

Recently, the popularity of group housing systems for calves has increased (Wójcik et al., 2012). Group housing is desirable under an animal welfare perspective because it improves cognitive performance (Gailard et al., 2014), offers more space for movement, and provides better opportunities for social behavior (Jensen and Kyhn, 2000; Chua et al., 2002; von Keyser-

lingk et al., 2009). De Paula Vieira et al. (2010) found that preweaned calves housed in pairs consumed more starter and vocalized less in response to weaning than individually housed calves. Intake of starter and ADG are significantly higher in calves paired soon after birth than in late-paired calves (Costa et al., 2015). Some studies claimed that morbidity (Le Neindre, 1993; Hanekamp et al., 1994; Svensson et al., 2003; Svensson and Liberg, 2006; Marcé et al., 2010; Cobb et al., 2014) and mortality (Le Neindre, 1993; Gulliksen et al., 2009b) are higher in group-housed calves than in individually housed calves. These findings, however, depend on many factors such as feeding regimen, management, and environment (Losinger and Heinrichs, 1997; Cobb et al., 2014). Hänninen et al. (2003) and Babu et al. (2009) found a lower incidence of diarrhea in group-reared calves compared with individually reared calves. Kung et al. (1997) observed fewer days of medication in calves raised in a group pen as opposed to individual hutches. The time to manage a calf in a hutch was 10-fold compared with the group pen. Bernal-Rigoli et al. (2012) observed greater DMI and final BW in group-housed calves compared with individually housed calves. Losinger and Heinrichs (1997), Svensson and Liberg (2006), and Babu et al. (2009) all concluded that housing calves in small groups compared with individual housing or large groups was beneficial for calf health and growth.

Open Range

Calves in cow-calf operations for beef production are often kept on open range where they are directly exposed to local climate and weather, potentially resulting in extreme heat or cold stress. Different structures can help to protect them from climatic conditions, ranging from natural structures (e.g., trees) over simple constructions (e.g., shelter, windbreaks, shades) to special appliances (e.g., fans, sprinklers).

During cold temperatures, protection from wind and the provision of a dry lying area and adequate feed are important (Webster, 1974). A common method to mitigate cold stress is the provision of shelter (Mader, 2003; Van Iaer et al., 2014). Holmes et al. (1978) found that the availability of a shelter resulted in increased weight gains in dairy heifers during winter. Without shelter, the ground is likely to become muddy during periods of high precipitation. Mud can lead to a decreased feed intake if cattle have to walk through it to reach their feeding place (Webster, 1974). Whereas partially enclosed shelters in temperate regions protect animals from cold and hot weather, in tropical climates closed shelters are not recommended because they obstruct natural air flow (Da Silva, 2012; Van Iaer et al., 2014).

Windbreaks act as a barrier, reducing wind speed and thus convective heat loss (Olson and Wallander, 2002; Van Iaer et al., 2014). Typically, they offer protection from wind along a distance of 5 to 10 times their height (Mader, 2003). The amount of time animals spent behind a windbreak was found to be correlated with wind speed, but not with ambient temperature (Olson and Wallander, 2002). With hot temperatures, however, windbreaks can impair airflow and increase heat stress, resulting in a decreased weight gain of feedlot calves (Mader et al., 1997).

Shades protect animals from direct solar radiation and mitigate heat stress (Mitlöhner et al., 2001; Mader, 2003). Silanikove (2000) recommended providing shade to animals in regions where typical summer temperatures exceed 24°C. The provision of shade can result in increased weight gains and feed intake (Mitlöhner et al., 2001); however, study results are not unanimous (Coleman et al., 1996; Sullivan et al., 2011). Other cooling methods include sprinkling, misting, and fans. Although many cooling methods have been suggested for adult cattle (Armstrong, 1994; Mitlöhner et al., 2001; West, 2003; Collier et al., 2006; Nienaber and Hahn, 2007; Schütz et al., 2011), literature evaluating cooling methods for calves is scarce. Nonetheless, it is likely that the same methods that have proven to alleviate heat stress in adult cattle, for example, different combinations of shade, sprinkling, and fans (Collier et al., 2006; Nienaber and Hahn, 2007; Schütz et al., 2011), are also effective for calves.

Calf Hutches

Davis et al. (1954) were among the first researchers studying outdoor individual portable pens and their beneficial role in controlling diseases. They argued that individual outdoor housing offered better hygienic conditions and a lower risk of infection with pathogens for respiratory disease and diarrhea. Today, keeping calves outdoors in pens, hutches, or igloos is a common practice all over the world (Hoshiba, 1986; Schäffer and von Borrell, 2008; Walker et al., 2012). Lower mortality rates (Davis et al., 1954; Waltner-Toews et al., 1986; Wójcik et al., 2012), reduced incidences of respiratory and gastrointestinal diseases (Davis et al., 1954; Okamoto et al., 1993; Nilsson, 2012; Wójcik et al., 2012), as well as higher weight gains (Davis et al., 1954; Richard et al., 1988) were recorded in calf hutches compared with housing in heated stables. Some authors, however, found no or only minor performance differences between both husbandry systems (Jorgenson et al., 1970; Hanekamp et al., 1994). Disadvantages of individual outdoor hutches include the lack of social

contact between calves and increased labor cost (Kung et al., 1997).

Hutches and igloos should have a radiation-reflecting surface and be placed with the opening away from the weather side on well-drained ground, preferably under a roof or cover. During winter, only fully dried newborn calves should be placed in outdoor hutches and sufficient dry bedding should be offered (Callan and Garry, 2002; Schäffer and von Borrell, 2008). Several studies analyzed the effect of calf hutch type and material on hutch microclimate, calf performance, and thermal physiology. Macaulay et al. (1995) compared 3 housing types during fall and found that enclosed molded polyethylene domes had the warmest microclimate, followed by conventional wooden hutches and thermomolded opaque polymer hutches. Roof material seemed to have only a minor influence on the thermal comfort of calves (Kawabata et al., 2005; Fonseca et al., 2012).

Air temperature inside hutches is correlated with ambient air temperature but rises with direct solar radiation (Hoshiba, 1986; Spain and Spiers, 1996; Kawabata et al., 2005). Hoshiba (1986) analyzed the microclimate in fiber-reinforced plastic calf hutches during the Japanese winter and recorded temperature and wind speed. Whereas the inside temperature was only 2.5°C higher on average than the outside temperature, wind speed in the hutches was reduced considerably. The mean occupancy rate (ratio of time a calf spent inside the hutch to 24 h) was 85 to 90%. Occupancy rates of the hutches were positively correlated with high wind speed. Hill et al. (2011) studied climatic parameters inside polyethylene hutches in Ohio during the summer and found the temperature to be 2°C higher and the relative humidity to be 8°C higher than outside. High relative humidity can cause condensation and result in wet walls, bedding, and hair coat (Abshoff and Steimle, 1983). This suggests that synthetic hutches provide a microclimate that is likely beneficial in cold, rainy, or windy conditions, but could be disadvantageous under hot or humid conditions.

The microclimate in calf hutches can be modified with the help of simple tools, for example by installing fans (Hill et al., 2011), by providing supplemental shade to prevent heat stress (Coleman et al., 1996; Spain and Spiers, 1996; Kawabata et al., 2005), or by elevating one side of the hutch to improve air exhaust (Moore et al., 2012). In a hot climate, however, these methods provide only a limited alleviation of the heat stress effect (Coleman et al., 1996).

In accordance with the increased trend toward group housing, hutches and igloos for groups of calves also have gained in popularity (Nilsson, 2012; Wójcik et al., 2012). Wójcik et al. (2012) compared group housing of

calves in igloos and in traditional barns and confirmed the advantages of outside housing for calf groups. Calves kept in group igloos exhibited higher weight gains and lower incidence of respiratory disease. Further research is still necessary to fully understand the subtleties of climatic conditions in group hutches.

Indoor Housing

Calves are often housed in barns, especially in regions with a cold climate (Webster, 1974; Klein-Jöbstl et al., 2014). For example, in Canada 80% of preweaned calves are kept in the main barn and 12% in a separate barn (Vasseur et al., 2010).

Basic types of indoor housing systems include closed barns, which are mechanically ventilated, insulated, and often possible to heat, and open, naturally ventilated stables (Hanekamp et al., 1994). Seedorf et al. (1998) recorded climatic conditions over more than 2 yr in 329 livestock buildings in Northern Europe. Calves were predominantly housed in naturally ventilated barns, where the climate was correlated with the outside climate and exhibited a seasonal pattern. The difference between inside and outside temperature decreased with increasing stocking density (Wagner-Storch and Palmer, 2002). Hanekamp et al. (1994), Ertugrul et al. (2000), and Svensson and Liberg (2006) compared open with closed barns as housing options for calves. They found a lower mortality rate, higher growth rates during the rearing period, and a higher feed intake in the open barn.

The microclimate inside a stable is an important component of the overall climatic conditions and is determined by the following factors: air temperature, temperature of stable surfaces, humidity, wind speed, and concentration of noxious gases, dust, and microbes. Potentially noxious gases include CO₂, carbon monoxide, NH₃, H₂S, and methane. A temperature of 16 to 20°C for calves with a BW of up to 60 kg and 10 to 20°C for calves weighing 60 to 150 kg are recommended by the German Institute for Standardization (DIN, 1992). Relative humidity should be 60 to 80% in mechanically ventilated stables and 40 to 70% in heated stables (DIN, 1992).

One of the many risk factors for respiratory disease is poor air quality. Especially in closed barns without proper ventilation, air quality, pathogen concentration, and associated diseases are often problematic (Barrington et al., 2002; Lago et al., 2006). Many airborne bovine viruses (e.g., bovine herpesvirus 1, bovine parainfluenza virus type 3, bovine respiratory syncytial virus, and bovine viral diarrhea virus) and gram-negative bacteria are hydrophobic and survive better in dry air, whereas increased survival time of most other

pathogens is associated with high humidity (Callan and Garry, 2002; Nordlund, 2008). Pritchard et al. (1981) established a link between air quality and incidence as well as severity of bovine respiratory disease (BRD) in confined sheds. In sheds equipped with an air filtration device, airborne bacterial concentration, antibiotic treatment for BRD, and area of lung consolidation at slaughter were reduced significantly compared with the control treatment (no air filtration). Weight gain was reduced in diseased calves. Lago et al. (2006) evaluated the effect of air quality on the respiratory health of calves in 13 naturally ventilated barns during winter (average temperature 4°C). High bacterial density, physical contact between calves, and a low nesting score (indicative for shallow depth of bedding) were associated with an increased prevalence of respiratory disease. Therefore, the authors recommended providing sufficient bedding to reduce cold stress in calves. Nonnecke et al. (2009) observed higher respiratory scores and a higher quantity of prescribed antibiotics in calves kept in a cold, wet environment than in a warm, dry environment. Brscic et al. (2012) investigated the prevalence of BRD in veal calves in a cross-sectional study on 174 farms in Europe. The main risk factors identified were cold climate, mechanical ventilation, and drafts. Further studies evaluating the incidence of respiratory disease in different housing systems are listed in Table 1.

Diarrhea is another common disease in calves. Many enteric pathogens are transmitted by the fecal-oral route; however, some infectious agents are also transmitted through aerosols. Environmental risk factors include climatic conditions (Barrington et al., 2002; Gulliksen et al., 2009a), housing (Gulliksen et al., 2009a; Klein-Jöbstl et al., 2014), stocking density (Frank and Kaneene, 1993; Barrington et al., 2002), and hygiene (Frank and Kaneene, 1993; Klein-Jöbstl et al., 2014). Still, the influence of the housing system on diarrheal incidence is less obvious than on the incidence of respiratory diseases (Table 1). Housing on noncontaminated ground, appropriate air quality, and ventilation are important for the enteric health of calves (Barrington et al., 2002). Hänninen et al. (2003) found a lower incidence of diarrhea in preweaned calves housed indoors in small groups compared with calves housed outdoors with or without shelter. Klein-Jöbstl et al. (2014) observed a greater odds ratio for diarrhea in Austrian dairy calves kept outdoors in igloos than in calves kept in individual pens in a barn. This observation was possibly contributed to the low temperatures and temperature fluctuations the igloo-raised calves were exposed to.

Frequent ventilation of barns is essential to supply fresh air and to minimize the amount of humidity and

airborne contaminants in the barn air. Pathogen concentration and the amount of pathogens inhaled were shown to decrease with air temperature (Callan and Garry, 2002; Nordlund, 2008). Hillman et al. (1992) installed a positive pressure ventilation system in a calf nursery that filtered air particles larger than 0.5 μm and supplied fresh air to the nursery depending on interior temperature, humidity, and ammonia level. They concluded that the ventilation system mimicked outside air conditions and greatly reduced respiratory disease in calves. A minimum air exchange rate of 6 changes per hour at a capacity of 6 m^3 per calf (Wathes et al., 1983) or 0.35 $\text{m}^3 \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$ should be reached. Depending on the input variables, much higher (10 to 15 $\times$ minimum rate) air changes might be necessary during summer (Turnbull, 1980; Charles, 1994). Whereas appropriate ventilation is necessary to control humidity and airborne pathogens, drafts with air velocities of over 0.2 m/s with low temperatures and over 0.6 m/s with high temperatures should be avoided (DIN, 1992). In winter, there is often a tradeoff between supplying fresh air and maintaining an adequate temperature (Callan and Garry, 2002; Nordlund, 2008). With very low outside temperatures, supplementary heating might be necessary (Turnbull, 1980). Nordlund (2008) recommended the use of positive-pressure ventilation systems to ensure a sufficient supply of fresh air in individual calf pens. This can be achieved by installing a fan that supplies external air to a distribution duct system, which delivers the fresh air to the individual pens.

In conclusion, popular housing systems for raising dairy calves are currently being challenged and more group-housing options are being explored. Enclosed stables allow for the greatest modification of outdoor climate, but it is generally agreed that outdoor housing offers better air quality and hygienic conditions. In open barns it is important to offer calves a draft-free microclimate with adequate bedding.

CONCLUSIONS

The discussion of housing systems and disease incidence in this review is limited to climatic aspects and does not intend to cover the full complexity of these subjects. Whereas various studies have been published on thermoregulation or thermic stress in general, this review is focused on the influence of climatic conditions on the performance and health of calves. Thermoregulation in calves is similar to that in adult cattle, but young calves are more prone to heat loss. Vital calves are born with functional thermoregulatory mechanisms and are remarkably cold tolerant under adequate management conditions. In dystocial calves, heat generation mechanisms are often impaired. Under cold conditions,

the feeding regimen should provide sufficient energy for heat production. Thermic stress is observed in association with extreme temperatures and large temperature variations, but other variables such as relative humidity and wind speed might also contribute to thermic stress. Whereas the tolerance of calves toward cold and the tolerance of adult cattle or dairy cows toward heat is well researched, studies regarding the thermoregulation of calves under hot conditions are scarce. Housing reduces the effect of climate on calves and can provide them with a beneficial microclimate. Cold stress in outdoor housing systems can be reduced by offering shelter or windbreaks. Limited results for alleviating heat stress can be achieved by simple measures, such as the provision of shade and easily accessible drinking water. Depending on the housing system, additional thermic stress relieving strategies might be warranted. Common individual housing systems for raising dairy calves are currently being challenged. Group housing is becoming more popular and desirable with regard to animal welfare and health aspects. More research is required to fully understand the ideal housing system for calves under different environmental and management conditions. Whatever the housing system, it is essential to offer calves a clean and dry environment with shelter from drafts, precipitation, and extreme solar radiation.

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