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Review Article

EFFECT OF HEAT STRESS ON LIVESTOCK REPRODUCTION

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ABSTRACT

In most livestock, heat stress has deleterious effects on physiological, nutritional, and reproductive functions. Exposure of livestock to a hot environment causes an increase in their body temperature. Heatstress has negative impact on reproductive traits of livestock.These include reduction inspermatogenesis in males, while in females it adversely affects oocyte development, oocyte maturation, implantation rate, early embryonic development, fetal and placental growth, and lactation.Heat stressalso causes a decrease in the length and intensity of estrus as well as decreasing pregnancy rate.Mostly effects of heat stress on gametes and the early embryo involve increased production of reactive oxygen species (ROS).Therefore, it is important to understand the effects of heat stress on reproductive functions in order to improve the livestock production. Identification and evaluation of the adverse effects of thermal stress on reproductive traits help us to design different measures to prevent heat stress and improve the livestock's reproductive functions. Theimpact of thermal stress on the reproductive functions of livestockis discussed in this paper.

Keywords : Embryo, Gestation, Heat stress, Livestock, Oocyte, Reproduction, Spermatogenesis

Climate change is one of the major threats for the sustainability of livestock production systems in tropical countries.The effect of climate change on animal health and production may be due to changes in environmental conditions *viz*. air temperature, relative humidity, precipitation, frequency and magnitude of extreme events (Gaughan *et al.,* 2009; Lacetera, 2019). Fifth assessment report of Inter-governmental Panel on Climate Change (IPCC) 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). Climate change has a great impact on the reproductive activity of livestock. These effects are mediated by induction of heat stress conditions in livestock. Adverse effect on animal's reproductive performance depends on intensity and duration of heat stress (Lacetera, 2019).

Livestock animal are homeothermic and are able to maintain a constant body temperature, regulating production of heat by their metabolism and the losses with the surrounding environment. As environmental temperature changes, the animals adjust their physiology and behavior in an attempt to keep their body temperature constant (DeShazer *et al.,* 2009). Livestock have optimal temperature zones for production within which no additional energy above maintenance is expended to heat or cool the body.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).Normally, animals maintain a body temperature above the surrounding ambient temperature which allows them to dissipate heat through three mechanisms requiring a thermal gradient (e.g., conduction, convection, and radiation). When the thermal environment exceeds the animal's body temperature these routes of heat exchange are lost, and heat loss is through evaporative routes (e.g., sweating and panting). These require a vapor pressure gradient and dictate that relative humidity is a major factor controlling rate of evaporative heat loss.

Elevated environmental temperature and relative humidity are the primary factors that cause heat stress in livestock. Combined effect of high ambient temperature and high humidity results adverse effect on reproductive performance of livestock (Sinha *et al.,* 2017). Sere *et al.* (2008) reported that heat stress has adverse effects on the productive, reproductive and health performances of dairy animals. Heat stress is a major factor contributing to the decline in fertility in lactating dairy cattle (Garcia-Ispierto *et al.*, 2007) and buffaloes (Dash *et al.*, 2015). Several studies reported 20 to 30% reduction in conception (Schuller*et al.*, 2014) and pregnancy rate (Khan *et al.*, 2013) in hot climatic condition. Heat stress can be quantified through formulating temperature humidity index (THI). The THI is determined by equation from the relative humidity and the air temperature and is calculated by formula:THI = 0.72 (W+D) + 40.6; whereW = Wet bulb temperature (^{o}C) and D= Dry bulb temperature (^{o}C).

As the environmental temperature elevates, evaporative cooling to dissipate body heat increases. However, high relative humidity during hot and humid weather reduces the effectiveness of evaporative cooling. The THI values of 70 or less are considered comfortable, 75-78 stressful and a value greater than 78 causes extreme distress with lactating cows being unable to maintain thermo-regulatory mechanisms to maintain normal body temperature.Humidity is the limiting factor of heat stress in humid climate, whereas dry bulb temperature is the limiting factor of heat stress in dry climates (Bohmanova *et al.,* 2007).

The involvement of heat stress as an inducer of

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oxidative stress has been acknowledged (Mujahid *et al.*, 2005; Lin *et al.*, 2006). Oxidative stress is defined as the presence of reactive species in excess of the available antioxidant capacity of animal cells (Halliwell and Whiteman,2004). Exposure of animals to elevated temperatures accelerates mitochondrial respiration and has been shown to increase reactive oxygen species (ROS) formation (Heise *et al.,* 2003; Keller *et al.,* 2004). Excess ROS production by intensively respiring mitochondria is held responsible for cellular damage expected upon exposure of an ectotherm to warming (hyperthermia) and heat stress (Abele *et al.,* 2002). Singh *et al.* (2013) reported breed differences in cellular stress markers, antioxidants, and significant numbers of genes (HSP70, MMPs, iNOS, Caspase and Bcl-2 family) of diverse biological functions and apoptotic responses to heat stress.In livestock,heat stress may exacerbate oxidative stresses which reduce their reproductive performance. The purpose of this paper is to describe the consequences of heat stress on different reproductive traits in livestock. Therefore, understanding how heat stress affect reproductive traits offer opportunities for improving livestock reproduction and production processes.

EFFECT OF HEAT STRESS ON REPRODUCTION

Reproductive functions of livestock are vulnerable to climate changes and both female and males are affected adversely. The livestock species which are more vulnerable to climatic changes are cattle and buffaloes. Sheep and goats can withstand the stress to some extent. Heat stress is a major contributing factor for low fertility in livestock.

EFFECTS ON MALE REPRODUCTION:

Spermatogenesis

Spermatogenesis is a complex biological process take place in the seminiferous tubules of testis. The testis is suspended in a scrotum outside the body in order to keep the temperature lower than core body temperature, which is required for normal spermatogenesis. In mammals, the testis temperature must range from 2 to 8°C below body temperature to ensure successful spermatogenesis (Senger, 2003; Banks *et al.*, 2005). Males are more susceptible to the pooled effect of high ambient temperature, relative humidity, solar radiation and the wind, which reduces both the quantity and quality of sperm production, thereby decreasing the male fertility (Rahman *et al.*, 2013; Dash *et al.*, 2016).

Temperature difference is required for optimal reproductive function (Banks *et al.*, 2005). Increases in scrotal temperature disrupt spermatogenesis and negatively impacts testicular function (Rasooli *et al.*, 2010) ultimately causing infertility (Paul *et al.*, 2008). Lower temperature is maintained in testis by a cooling system comprising the scrotum, pampiniform plexus, and muscles (Senger, 2003).Elevated testis temperatures, increases the testicular metabolism without increase in blood supply, resulting in local hypoxia and deleterious effects for the tissue (Aitken and Roman, 2008).

Heat stress adversely affects testis function in numerous animal species, including cow (Roth *et al*., 2000), pig (Malmgren and Larsson, 1984), sheep (Boland *et al.*, 1985), and horses (Love and Kenney, 1999). Heat stress eliminates spermatogonial germ cells in the seminiferous tubules, which results in decreased sperm density (Rasooli *et al.*, 2010). Harmful effects of exposure to heat are responsible for the azoospermia or oligospermia in many animal species. Paul *et al.* (2009) reported that transitory mild testicular hyperthermia results in temperature dependent germ cell death and a complex stress response, including oxidative stress and hypoxia. Heat stress also affects the endocrine function and biochemical status of male animals. Elevated temperature increases the level of oxidative marker such as thiobarbituric acid reactive substances (TBARS), and decreased glutathione peroxidase (GPx) level which is an antioxidant enzyme in bovine seminal plasma (Kowalowka *et al.*, 2008). Marti *et al.* (2007) reported similar changes in rams. Some evidence showed that heat stress to testis with acute scrotal heating decreases not only semen quality, but also decreases embryo quality after fertilization in female mice (Yaeram *et al.*, 2006, Paul *et al.*, 2008) as well as fetal growth (Jannes *et al*., 1998). Heat stressalso has endocrine effects, reducing the plasma luteinizing hormone (LH) level in bulls (Rhynesand Ewing, 1973) and increasing the plasma testosterone level in boars (Murase *et al.*, 2007). The quantity and quality of semen vary with season of the year, species, breed, and locality. In heat stress semen characteristics are inferior or in many cases semen not ejaculated (Hamilton *et al.*, 2016).

Cryopreservation of semen

Semen cryopreservation is a technique to preserve sperm cells which is an integral part of the cattle breeding industry (Curry, 2000).In agriculture, semen cryopreservation is used for genetic improvement of domestic species, to preserve rare breeds, well adapted to environmental changes, and preservation of endangered species (Holt, 1997; Andrabi and Maxwell, 2007). Semen cryopreservation contributes to the expansion of reproductive techniques, such as artificial insemination (AI) and *in vitro* fertilization (Medeiros *et al.,*2002).

Season is one of the important factors that influence the variation in semen quality and fertility. During summer, thyroxin secretion declines leading to reduced intake of feed by the animal, subsequent metabolism (Madan, 1985) and is responsible for reducing production of sperm (Zafar *et al.,* 1988). Rajoriya *et al.* (2013) reported that ejaculate volume, sperm concentration, mass-motility, progressive motility, vigor and morphological sperm defects were significantly influenced by season. Several other studies have shown seasonal variations in bull semen quality under varying environmental conditions such as environmental

temperature, humidity, photoperiod and quality of basal diet (Parkinson, 1985; Quereshi *et al*., 1995; Mathevon *et al*., 1998). Sperm concentration lowers in the fall and there is increase in the number of abnormal sperms in summer, and the lower percentage of fertile mating reported in Shorthorn cattle in summer (Phillips *et al*., 1943). Prolonged heat stress during summer months can reduce the quality of semen produced. Some bulls are more susceptible to heat stress than others. A reduction in a bull's libido during heat stress will severely limit the semen harvest (Marshall, 1984). Cryopreservation of Tharparkar bull semen in summer and winter season did not show any definite pattern in relation to enzymatic changes (Rajoriya *et al.,* 2013). However, better membrane integrity as reflected by higher HOST positive spermatozoa was recorded in winter season in comparison to summer season in the fresh ejaculates of Tharparkar bulls (Rajoriya *et al.,* 2013). However, Rajoriya *et al.* (2014) reported non-significant differences in the mRNA expression of HSP 70 and HSP 90 during winter and summer season indicates presence of similar type of stress resistant spermatozoa in both the season. Kumar *et al.* (2016) revealed that the effect of season significantly influences the ability of buck spermatozoa to withstand the freezing and thawing process. The spermatozoa from ejaculate collected during autumn were more cryosensitive than those collected during winter (Kumar *et al.*, 2016).Tuli and Holtz (1995) reported that semen freezing during winter have a higher proportion of motile spermatozoa in Boer buck. Barranco *et al.* (2013) found better freezabilty of boar semen collected during winter and spring than in summer and autumn in term of motility, viability, and abnormalities.

EFFECTS ON FEMALE REPRODUCTION:

Reproductive patterns and estrus detection

Heat stress reduces the duration and intensity of estrus in dairy cattle. For example, in summer, motor activity and other manifestations of estrus are reduced and the incidence of anoestrus and silent ovulation are increased (Hansen, 1997). Pennington *et al.* (1985) reported that above effects lead to a reduction in the number of mounts in hot weather compared to cold weather, leading to poor detection of estrus. Thermal stress negatively affect estrus expression/ovarian activity and conception rate in cattle and buffaloes (Upadhyay *et al.*,2009). Heat stress reduces the degree of dominance of the selected follicle and this can be seen as reduced steroidogenic capacity of its theca and granulosa cells and a fall in blood estradiol concentrations (Hansen, 1997). During summer low hormonal levels also influence the diurnal pattern of estrus expressions and number of heat symptoms in buffaloes (Madan and Prakash, 2007). Kaur and Arora (1984) reported that low level of nutrition coupled with high environmental temperature stress has been attributed to long anestrus periods in buffaloes. The effect may be much more pronounced in buffaloes, temperate and crossbred breeds compared to indigenous breed of cattle due to poor adaptability of these species to tropical climatic conditions (Upadhyay *et al.*, 2009). Neble *et al*. (1997) also reported similar findings in Holstein cows, where number of mounting episodes per estrus was only 4.5 in summer, compared to 8.6 in winter. Wolfenson and Roth (2019) reported that heat stress during the summer disrupts several reproductive processes, resulting in a pronounced depression of conception rate in dairy cows worldwide. Therefore, heat stress causes a decline in successful artificial inseminations and pregnancies.

Folliculogenesis

Folliculogenesis is a continuous process of growth and regression of a group of antral follicles, one of which develops to attain pre-ovulatory stage (Lucy *et al.*, 1992).The follicle destined to ovulate, emerges as an antral follicle 41.5 days before ovulation (Lussier *et al.*, 1987). Folliculogenesisis susceptible to heat stress. Therefore, heat stress during the folliculogenesis has the potential to compromise the oocyte, either because of direct actions of elevated temperature on the oocyte or because of alterations in follicular function that could compromise oocyte quality. Putney *et al.* (1988) reported that first-wave of dominant follicle in heat-stressed lactating cows was found to be smaller in diameter and to contain less fluid than that of controls cows on day 8 of the cycle. Some investigators employed ultrasonography to examine follicular growth. Badinga *et al.* (1993) observed that acute heat stress reduced the size of the first wave dominant follicle by day 8 of the estrous cycle and the follicle contained less follicular fluid than that of non-heat stressed cow. Furthermore, heat stress reduced granulosa cell viability, aromatase activity, and androstenedione production in theca cells from day 7 first-wave dominant follicles (Lew *et al.*, 1993).Wilson *et al*. (1998) also observed reduction in follicular size in heat stressed cattle and related it to decreased steroidogenesis within the theca cells, granulose cells or both. The possible mediators of heat stress response were reduced variability of granulosa cells or more specific changes in steroidogenic enzyme aromatase activity in granulose cells (Wolfenson*et al.*, 1997). Hooda *et al.* (2011) revealed that heat stress inhibit follicular growth, decrease proestrus rise in estradiol-17β and induce smaller size of the second wave dominant follicle. de S Torres-Junior *et al.* (2008) demonstrated that in Gir cows, heat stress exerted a delayed effect on reproductive functions. Delayed effect manifested by an increased incidence of large follicles, more follicular co-dominance and reduction in estrous cycle length, progesterone concentration and oocyte developmental capacity. Heat stress induced co-dominance that may compromise oocyte quality has been reported in cow (Sartori *et al.*, 2004) and goats (Chandra *et al.*, 2007).

Oocyte competence

The oocytes in ovarian pool are most sensitive to elevated temperature. Heat stress reduces oocyte

developmental competence by affecting growth and maturation through an increase in oxidative damage and apoptotic cell death, as well as by inducing irreversible changes on cytoskeleton and meiotic spindle (Hansen, 2009). Edwards and Hansen (1997) reported that elevated temperature may negatively affect the oocyte growth, protein synthesis and the formation of transcripts required for subsequent embryonic development. In Holstein cows, oocytes collected during the summer exhibited a delay in the two first embryonic divisions (Gendelman *et al.*, 2010).In summer, heat stressed Holstein cows exhibit lower proportion of oocytes and cleaved embryos that could have otherwise developed into blastocysts by day 8 (Al-Katanani *et al.* (2002). Other studies showed a reduced proportion of oocytes that were fertilized and further developed to the blastocyst stage under heat stress (Roth *et al.*, 2001). A period of two to three estrous cycles was found to be required for recovery from summer heat damage, indicating a long-lasting effect of heat stress on the ovarian pool of oocytes (Roth *et al.*, 2001; Roth, 2017).

Oocytes cultured at 41°C arrested their development at metaphase-1 stage (Roth and Hansen, 2005). Oocytes exposed *in vitro* to different temperatures (38.5, 40 and 41°C) showed altered maturation, namely a decreased in the percentage of mature oocytes retrieved when cultured at 40 and 41°C, compared with the proportion obtained during culture at 38.5°C (Wilson *et al.*, 1998). Edwards and Hansen (1997) also demonstrated that under elevated temperature conditions the oocytes evidence a decrease in protein synthesis, disturbed microfilament and microtubule architecture, disorganization of the meiotic spindle and increased incidence of induced cell death due to apoptosis. Moreover, the elevation of temperature increases the number of apoptotic cells in 2-cell-stage embryos (Fear and Hansen, 2011). This evidence indicates that heat stress directly damages early stage embryos and leads to decreased developmental competence.

Exposing oocytes to 41 °C during maturation increased the proportion of oocytes with fragmented DNA (Ferreira *et al.,* 2016). 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). Another seasonal study reported the lower expression of genes associated with oocyte maturation (FGF16, GDF9) in cows during the summer (Ferreira *et al.,* 2016).The expression of apoptotic genes was also higher in repeat breeder cows during the summer (Ferreira *et al.*, 2016). Pavani *et al.* (2016) reported differential expression of stress related genes: Cx43, DNMT1, and HSPA14 in embryos developed from oocytes collected during the summer, relative to those collected during the winter.

Embryonic growth and development

The intrauterine environment is also compromised in cows that are heat stressed. These changes inhibit proper embryonic development and increase early embryonic loss. Heat stress adversely affects pre-attachment stage embryos; however, magnitude of the effect decreases as embryos develop. Effect of heat stress causes alterations in the follicle and its enclosed oocyte. Preimplantation embryos at early stages of development are highly sensitive to heat stress (Hansen, 2013). Preimplantation embryos are also sensitive to elevated temperature, in a stage-dependent manner (Hansen, 2007). Therefore, embryo transfer at day 8, to bypass the thermo sensitive developmental stages, has been suggested by Hansen (2013). Some reports suggest that oocytes are more susceptible to the elevation of temperature during the first 12 hours of maturation because the exposure of oocytes to heat stress would hasten the progress of cytoplasmic and nuclear maturation (Edwards *et al.*, 2005; Roth and Hansen, 2005). Embryos at later developmental stages (i.e., morula, blastocyst) are more resistant to heat stress. Interestingly, heat shock differentially affects embryonic development in different breeds, with a moderate negative effect in *Bos indicus* (Hansen, 2007). The production of embryos by super-ovulation is often reduced and embryonic development compromised in hot season. Heat stress also affects endometrial prostaglandin secretion, leading to premature luteolysis and embryo loss. Most embryonic losses occur before day 42 in heat stressed cows.

Heat stress causes embryonic death by the interfering with protein synthesis, oxidative cell damage, reduction in successful pregnancy recognition and expression of stress-related genes associated with apoptosis. Deleterious effects of heat stress on the embryos being most evident in early stages of its development (Demetrio *et al.*, 2007). Ealy *et al.* (1993) revealed that exposure of lactating cows to heat stress after the 1st day of estrus has reduced the development of embryos to blastocyst stage after 8th day of estrus. Demetrio *et al.*(2007) also reported that either *in vitro* or *in vivo* exposure of embryos to high temperatures until day 7 (blastocyst stage) lead to lower pregnancy rates and higher rates of embryonic loss. Heat stressed embryo at the time of post-implantation period was found to be associated with fetal malnutrition and various other teratologic conditions in cows, which may eventuallyend up in embryonic death (Kadokawa *et al.*, 2012).

Fetal and placental growth

Maternal heat stress during gestation period has adverse effects on fetal and placental growth (Hansen, 2009).The mechanisms involved in this phenomenon have been best characterized in sheep. Maternal heat stress in sheep decreases placental weight (Vatnick *et al.*, 1991) and placentome size (Early *et al.*, 1991). Heat stress also causes reduced concentrations of placental hormones

in the blood (Wallace *et al.,* 2005).Heat exposure to mother after fertilization reduces the pregnancy rate and causes embryonic death before implantation (Ealy *et al.*, 1993;Ozawa *et al.,* 2002). Heat stress might disturb the intrauterine environment both for embryos and uterine tissue. Takahashi (2011) reported that the viability of uterine epithelial cells recovered from uterine flushing at the time of embryo collection in beef cows decreased in summer and embryo quality also tended to decline. Similar effects of maternal heat stress on placental function and fetal development occur in the cow (Collier *et al.*, 1982). Maternal heat stress in cow reduces the levels of placental hormones, which disturbs placental function and slows fetal development (Collier *et al.*, 1982). In cow, and presumably others species, reduced secretion of placental hormones as a result of heat stress can cause reduced milk yield (Wolfenson *et al.*, 1988). Heat stress also causes alterations in angiogenesis, which resulted in reduced blood perfusion in the placental vascular bed (Galan *et al.*, 2005). Therefore, inadequate nutrition for the neonate could conceivably be one aftereffect of maternal heat stress during gestation.

Lactation

Heat stress adversely affects the milk production and their composition in dairy animals, especially in high genetic merit animals (Upadhyay *et al.,* 2009; Wheelock *et al.,* 2010). During summer, an increase of body temperature significantly decreased milk production (Bohmanova *et al.*, 2007). Heat stress through physiological and nutritional effects diminished the milk production in cattle. Increasing air temperature and THI value above the critical thresholds level lead to decreased dry matter intake (DMI) and milk yield and also disturbance in physiology of animal (West, 2002). In response to heat stress dairy cows reduce feed intake leading to negative energy balance responsible for the drop in milk production (Wheelock *et al.,* 2010). Rhoads *et al.* (2009) reported that decrease in DMI by 0.85 kg per cow for every 1°C increase above the thermo neutral zone (TNZ) and decline in milk production by 36% due to shift in post absorptive metabolism and partitioning of nutrient. In pig, heat stress also reduced the feed intake thus milk production (Huynh *et al.*, 2005).

Zimbelman *et al.* (2010) reported a negative relationship between rectal temperature and milk yield of animals. Johnson *et al.* (1963) revealed that decrease in milk yield by 4 lbs/d per cow for every 0.55 °C increase above the rectal temperature of 38.6 °C. Baumgard and Rhoads (2013) reported that 50% drop in milk production in dairy animals is due to reduced feed intake and rest due to metabolic adaptations to heat stress as heat stress response markedly changes post absorptive nutrient metabolism. Heat stress cause decline in dry matter intake and feed conversion efficiency which directly affects the body condition and results in low milk yield (Wilson *et al.,* 1998). Heat stress during summer season significantly affects both milk quantity and milk constituents. Various components of milk such as fat (%), solid-non-fat, protein, casein and lactose contentare also affected. Heat stress can increase the somatic cell count indicating the reduction in quality of milk produced (Pragna *et al.,* 2017). Nardone *et al.* (1997) observed reduction in percentages of total protein, fat casein, lactose, lactalbumin, short and medium-chain fatty acids, IgG and IgA for the first four lactations.

Dairy breeds are more susceptible to heat stress than meat breeds, and higher milk producing animal had increased metabolic heat production and this causes more susceptibility to heat stress as compared to less milk producing animals (Dash *et al*., 2016). Heat stress during dry period reduces mammary cell proliferation which results in decreased milk production in subsequent lactation. During the dry period, heat stress adversely affects the function of the immune cell in lactating cows facing calving and also extended to the following lactation (Tao and Dahl, 2013).

CONCLUSION

Climate change has adverse effects on health status of livestock and decreases the milk production and reproductive performance, resulting in huge economic losses. In most livestock, heat stress can have broad effects on most aspects of reproductive functions. Heat stress adversely affects male and female gamete formation and their functions. In male, heat stress negatively affects spermatogenesis by which diminished semen quality and quantity; while, in females, it adversely affects reproductive patterns and estrus expression, folliculogenesis, oocyte competence, embryonic growth and development, fetal and placental growth, and lactation. Heat stress reduces the milk production as well as their quality by altering various components of milk. Present review provides a clear insight into how heat stress affects reproductive physiology of both male and female livestock.

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