Chapter 4

Mitigation of the Heat Stress Impact in Livestock Reproduction

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Abstract

Heat stress affects the fertility and reproductive livestock performance by compromising the physiology reproductive tract, through hormonal imbalance, decreased oocyte quality and poor semen quality, and decreased embryo development and survival. Heat stress decreases the secretion of luteinizing hormone and estradiol resulting in reduced length and intensity of estrus expression, increased incidence of anoestrus and silent heat in farm animals. Oocytes exposed to thermal stress lose its competence for fertilization and development into the blastocyst stage, which results in decreased fertility because of the production of poor quality oocytes and embryos. Furthermore, low progesterone secretion limits the endometrial functions, and subsequently embryo development. In addition, the increased secretion of endometrial prostaglandin F2 alpha during heat stress threatens the maintenance of pregnancy. In general, the percentage of conception rate was found to be reduced by 4.6% for each unit increase in temperature humidity index (THI) above 70, and heat stress during pregnancy further slows down the growth of the foetus and results in lower birth weight. In tropical and subtropical regions, during hot days, the testicular temperature may increase and impair both the spermatogenic cycle and semen quality, which culminates in decreased bull fertility. The effects of heat stress on livestock can be minimized via adapting suitable scientific strategies comprising physical modifications of the environment, nutritional management and genetic development of breeds that are less sensitive to heat stress. In addition, the summer infertility may be countered through advanced reproductive technologies involving hormonal treatments, timed artificial insemination and embryo transfer, which may enhance the chances for establishing pregnancy in farm animals.

Keywords: antioxidants, cooling devices, estrus, fertility, shade, thermo-tolerant genes

1. Introduction

The performance, health, and well-being of livestock are strongly affected by climate. High ambient temperatures, high direct and indirect solar radiation and humidity are environmental stressing factors that impose a strain on animals. Among the environmental variables affecting livestock, heat stress seems to be one of the most intriguing factors hampering animal production in many regions of the world. Even though new knowledge on the animal responses to the environment continually arises, managing livestock to reduce the impact of climate remains a challenge. Considerable efforts are, therefore, needed from livestock researchers to counter the impact of environmental stresses on livestock production. Besides ensuring the livelihood security to our poor and marginal farmers, stress mitigation can also improve the economy of livestock industry as a whole. Hence, it is crucial to understand the impact of environmental stress on livestock production and reproduction. These efforts may help in identifying the appropriate targets for developing suitable mitigation strategies.

Thermal stress effects on livestock are of multifactorial nature. It directly alters and impairs the cellular functions in various tissues of the body and the redistribution of blood flow, as well as the reduction in food intake, which ultimately results in reduced production performance. Reproductive functions of livestock are particularly vulnerable to climate change; it has been established that large ruminants are more prone to heat stress compared with small ruminants [1]. Heat stress is the major cause for infertility and reproductive inefficiency in livestock, resulting in profound economic losses. Heat stress reduces the libido, fertility and embryonic survival in livestock and favors the occurrence of diseases in neonates with reduced immunity. Heat stress affects the fertility and reproductive performance of livestock species through compromising the functions of the reproductive tract, disrupting the hormonal balance, decreasing the oocyte quality, and thereby decreasing embryo development and survival [2–4]. In the tropical and subtropical regions, during the hot season, both the poor quality of oocytes and embryos results in decreased conception rate and subsequently with more days open resulting in huge economic losses to the dairy industry [5]. The high ambient temperature and relative humidity directly affect reproduction by altering or impairing various tissues or organs of the reproductive system of animal [6]. The threshold level of temperature humidity index (THI) for the high performance in terms of milk yield and reproduction is around THI 72 in tropical and subtropical climates. However, recent studies on THI in temperate climate emphasized that the THI lower than 68 is suitable for cattle performance and welfare [7].

This chapter is an attempt to cover in detail the impact of various heat stress factors on livestock reproduction, in both the female and male. Apart from these influences, the chapter also elaborates on available mitigation strategies directed to sustain livestock reproduction in the changing climate scenario.

2. Impact of heat stress on female reproduction

High environmental temperatures impair the female reproductive process at various stages of pubertal development, conception and embryonic mortality. Stress inhibits the reproductive

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performance of livestock species by activating the hypothalamic-pituitary-adrenal (HPA) axis, which subsequently excites the pituitary gland to release adrenocorticotropic hormone (ATCH) (**Figure 1**). The ACTH stimulates the release of glucocorticoids and catecholamines, which act extensively to alleviate the effect of stress. However, ACTH-stimulated glucocorticoid release is responsible for an inhibitory effect on the reproductive axis. Heat stress reduces the length and intensity of estrus, alters follicular development and increases the rate of apoptosis in the antral and pre-antral follicles. Extreme environmental temperatures delay the onset of puberty in male and female animals. Furthermore, heat stress during follicular recruitment suppresses the subsequent growth and development to ovulation [8]. Changes in the follicular growth disturb further progress and function of the oocytes [9, 10]. The chronic release of ACTH, such as the associated with heat stress, inhibits the ovulation and follicular development by altering the efficiency of follicular selection and dominance and glucocorticoids are critical to mediating this inhibitory effect on reproduction [11]. Further, high level of glucocorticoids during heat stress directly inhibits the meiotic maturation of oocytes, and, in addition, corticotropic releasing hormone (CRH) inhibits the ovarian steroidogenesis, derived of the decrease in the secretion of luteinizing hormone (LH). The consequent decrease in estradiol results in reduced length and intensity of estrus expression [12].

2.1. Reproductive hormones in female livestock

The reproductive hormones play a vital role as they regulate various stages of development and function in the female reproductive system. The high ambient temperature and solar

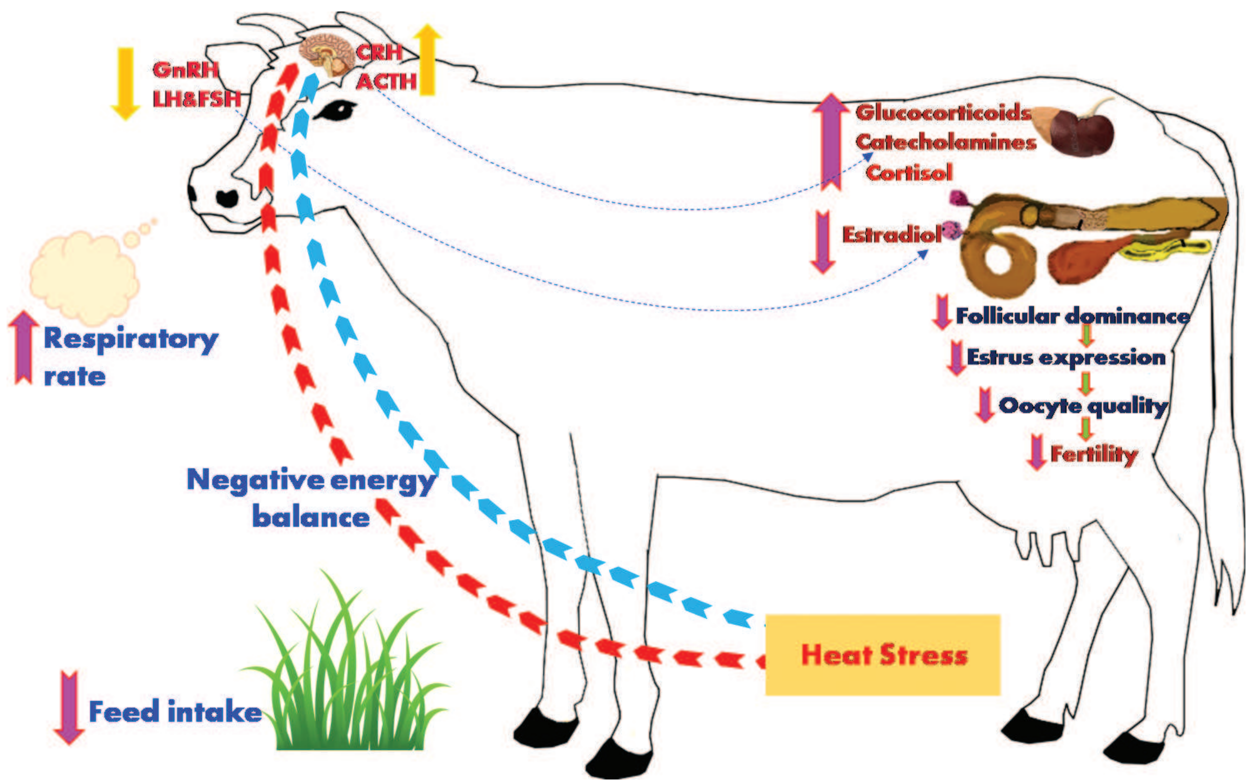

Figure 1. Impact of heat stress on female reproductive performance.

radiation as a result of climate change may affect the reproductive rhythm via the hypothalamic-hypophyseal-ovarian axis [13]. Various studies also revealed a significant negative correlation between environmental temperature and the reproductive hormone concentration, which in turn cause compromised reproductive efficiency in farm animals [14, 15]. The foremost important factors that regulate the ovarian activity are the gonadotropin-releasing hormone (GnRH), from the hypothalamus, and the gonadotropins (FSH and LH), from anterior hypophysis.

In cattle, the immediate 16 h exposure to a higher temperature (40°C) on day 12 of the estrous cycle lead to a significant reduction of GnRH-induced FSH secretion [16], whereas tonic FSH secretion was elevated probably due to reduced inhibition of negative feedback from small follicles [8]. Heat stress decreases LH pulse amplitude and frequency in cattle with low estradiol, thereby compromising the maturation and ovulation of the dominant follicles, while low tonic LH levels also hinder luteal development by inhibiting follicular growth and turnover in cyclic cows [2]. Furthermore, the decrease in the pre-ovulatory release of LH during heat stress reduced the expression of estrus behavior and delayed ovulation. Also in goats, exposition to high environmental temperatures induced lower follicular fluid and plasma estradiol concentrations and reduced LH receptor levels following lagged ovulation [8]. Estradiol secretion in the ovarian follicle is depressed under heat stress, primarily due to reduced theca cell androstenedione production associated with low 17α-hydroxylase expression. In addition, reduced granulosa cells aromatase activity and viability also contribute to poor estradiol secretion. In the case of dominant follicles, subsequent plasma progesterone concentrations are reduced during heat stress and result in the small size of ovulatory follicles with low tonic LH stimulation of luteinization and steroidogenesis [17]. Moreover, low progesterone secretion limits the endometrial function and subsequent embryo development. The increased level of circulating prolactin leads to suspension of estrous cycles and infertility during heat stress [18–20].

2.2. Follicular growth and development

Heat stress damages the developing follicles whenever the core body temperature exceeds 40°C [9]. Heat stress alters the follicular development by reducing steroid hormone secretion, which disrupts the oocyte growth, reduces the growth of dominant follicles and increased growth of subordinate follicles. Heat stressed lactating Holstein cows present smaller follicular diameter compared to non-stressed cows (14.5 vs. 16.4 mm, respectively) showed and also reduced fluid volume (1.1 vs.1.9 ml, respectively) [21]. In addition, heat stress was associated with reduced follicular dominance by prompting numerous large follicles with diameters above 10 mm, with prolonged dominance of ovulatory follicles [10]. Thus, the selection and dominance of normal follicles could be disturbed by high tonic follicular stimulating hormone (FSH) availability [2]. Low LH and the negative animal energy balance during summer prevent the maturation and ovulation of dominant follicles [17]. As the prolonged follicular dominance disrupts the normal oocyte maturation and reduces their developmental competence, the development of small dominant follicles during higher temperature results in ovulation of the infertile oocyte or subfunctional corpora lutea. The regression of the premature dominant follicle before attaining the larger size leads to a substantial reduction in ovulation percentage [8, 11, 17].

2.3. Effects of heat stress on estrus incidences

The seasonal cycle of reproduction in female animals is primarily controlled by the photoperiod, and it was found to be affected drastically by climate changes. Some studies proved the negative influence of heat stress on estrus incidence and duration and hence on estrus detection [6]. The length and intensity of estrus are inversely associated with the environmental temperatures, with higher temperatures triggering an increase prevalence of anestrus and silent heat in farm animals [18, 22]. A significant reduction in the interestrous interval was reported in Japanese black cattle during summer (21.5 days) compared to winter (23.4 days) [23]. Also, Bulbul and Ataman [24] report a decrease in estrus occurrences in cattle with an ambient temperature above 20.5°C. Likewise, decreased estrus duration and delayed onset of estrus were reported in heat stressed Bharat Merino ewes, which were attributed to abnormal LH pulsatility and lower estrogen synthesis during heat stress condition [25]. Malpura ewes exposed to multiple stresses (heat stress, nutritional stress, and walking stress) recorded lower estrous percentage and estrus duration in compared to control (41.7 vs. 66.67% and 14.4 vs. 32 h, respectively) [26, 27]. Similarly, a lower rate of estrus detection was reported in summer compared to spring and winter in dairy cattle. Contrasting to cattle, buffalos exhibit estrus when the ambient temperature is low, with THI value of less than 70 [1, 28].

In addition to ambient temperature, the humidity and solar irradiation also affected the expression of reproductive rhythm in buffaloes and cattle [29]. A diurnal rhythm of estrus behavior has been observed in the majority of Murrah buffaloes, with 60% of estrus exhibited between 22.00 and 6.00 h [28].

2.4. Sexual behavior

Sexual behavior acts as a core indicator of the reproductive activity in livestock females. It was found to be negatively influenced by environmental stressors like elevated temperature [30]. Reduced sexual behavior is reported in livestock during the hottest parts of the day. Wilson et al. [31] suggested that heat stress inhibits the follicular growth during the pre-ovulatory period of proestrus and reduces the intensity of estrus signs by decreasing the level of estradiol. Heat stress also modifies cow behavior, such as decreased walking time during estrus, which contributes to poor estrus detection in dairy cows during summer compared to winter [22]. Cows are less likely to exhibit standing heat during day time in summer months and often shows estrus at night hours when the ambient temperature is low [32]. Upadhyay et al. [28] reported that the low level of estradiol on the day of estrus also leads to poor expression of heat in Indian buffaloes during the summer period, favoring feeble estrus detection in buffalos during the summer season [29]. In cows, behavioral estrus is markedly reduced in summer, when THI is around 78 [28, 29, 33], while the incidence of anestrus and silent ovulation increases [34]. The cows in estrus mount more frequently during winter compared to summer, when detection of estrus is challenging. Furthermore, Japanese Black cattle exposed to heat stress showed lower locomotor activity during estrus, which was attributed to a reduced estradiol 17β production [23].

2.5. Effect on oocyte competence

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 [10]. The elevated temperature may negatively affect the oocyte growth, protein synthesis and the formation of transcripts required for subsequent embryonic development [35]. Reduced mRNA content and storage protein for early embryonic development along with altered membrane integrity affects signal transduction and protein transport. Therefore, prolonged follicular dominance leads to premature meiosis and aged oocytes with the poor developmental prospect. Incomplete dominance could result in ovulation of an aged follicle containing oocytes with reduced competence. Among other effects, incompetent oocytes become transcriptionally inactive by reaching a diameter of 110 μm and lose the ability to synthesize heat shock protein 70 (HSP70) in response to heat shock [36].

In summer, heat stressed Holstein cows exhibit lower proportion of oocytes and cleaved embryos that could have otherwise developed into blastocysts by day 8 [11]. 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 [31]. Oocytes cultured at 41°C arrested their development at metaphase 1 stage [37]. Other *in vitro* experiments 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 [35]. The protein impairment and the increased production of free radical in oocytes alter the zona pellucida layer and the oocyte cytoplasm which in turn impair sperm penetration. Therefore, reduced oocyte competence and stress induced oocyte lesions in the early stages of follicular growth result in poor fertility rate [2].

However, even though *Bos indicus* cows exhibited reduced oocyte quality during chronic heat exposure, they do not show any significant changes in the oocyte quality or competence during acute heat stress [38, 39]. This suggests that either the animal genetics or the length of heat stress may determine the impact of heat stress in cattle reproduction. Thereby, multifactorial mechanisms are involved in the reduction of fertility of domestic animals during heat stress [6].

2.6. Fertility

The high yielding lactating cows are more adversely affected by heat stress than heifers because of their increased metabolism, which generates greater internal heat production thus lowering their fertility rate in summer and autumn compared to winter periods [36]. Heat stress before insemination has been associated with decreased fertility in cattle and sheep [11]. Fertility decreases in buffaloes exposed to THI above 75 in subtropical climatic condition as compared to cattle, since buffaloes are more sensitive to heat stress [6]. The increase of uterine temperature by 0.5°C during hot days causes a decrease in the rate of fertilization [30] since in

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severely heat stressed cows most damages over the conceptus occur between estrus and day 7 of pregnancy [39].

Heat stress-related infertility is a current worldwide concern in the livestock industry, particularly in dairy cattle. A report reveals a higher percentage of reduction in conception rate during summer months as compared to cooler months [40]. The elevated environmental temperature on the day of insemination is negatively associated with conception rates [41–43]. Impaired conception was associated with heat stress in livestock, either during the breeding period or 42 days before and 40 days after insemination [42]. The conception rate in high yielding Israeli cows was 45% in winter and 20% in summer [2, 44, 45]. Also, Chebel et al. [46] reported a 20–27% drop in conception rates and a decrease in 90-day non-return rate to the first service in lactating dairy cows during summer. In dairy cows, the percentage of conception rate is reduced by 4.6% for each unit increase in THI above 70 and in practical reality, conception rate was often declined to less than 10% during summer [32, 47].

2.7. Embryonic growth and development

The embryonic loss is another important factor that affects fertility in cattle, and bovine embryos are sensitive to maternal heat stress during the first 2 weeks after breeding [17, 36]. A major source for a reduction in embryonic survival induced by heat stress may be due to the adverse effects of elevated body temperatures on developing zygotes and embryos. High ambient temperatures during oocyte maturation and ovulation or during the first 3–7 day of pregnancy reduced the embryonic viability and development. Although elevated temperatures affect the pre-attachment stage of embryos, the degree of the effect decreases as the embryo develops. 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. The 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 [39], the deleterious effects of heat stress on the embryos being most evident in early stages of its development [48]. *In vitro* or *in vivo* exposure of embryos to high temperatures until day 7 (blastocyst stage) is accompanied by lower pregnancy rates up to day 30 and higher rates of embryonic loss occurred on day 42 of gestation [48]. Embryos at day 1 are more susceptible to maternal heat stress than embryos at days 3–7. In addition, heat stressed embryo at the time of post-implantation period was found to be associated with foetal malnutrition and various other teratologic conditions in cows, which may ultimately culminate in embryonic death [22].

2.8. Impact on pregnancy

Heat stress negatively affects the ability of an animal to become pregnant through many mechanisms affecting fertilization, follicular development and early embryonic development (**Figure 2**). Ryan et al. [49] reported that when the rectal temperature of the animals increased from 38.5 to 40°C at 72 h after insemination, pregnancy rate decreased up to 50%. Amundson et al. [45] also found a significant reduction in the pregnancy rate in beef cattle during summer (62%) when the THI was equal to or above 72.9. Likewise, Amundson et al. [50] reported

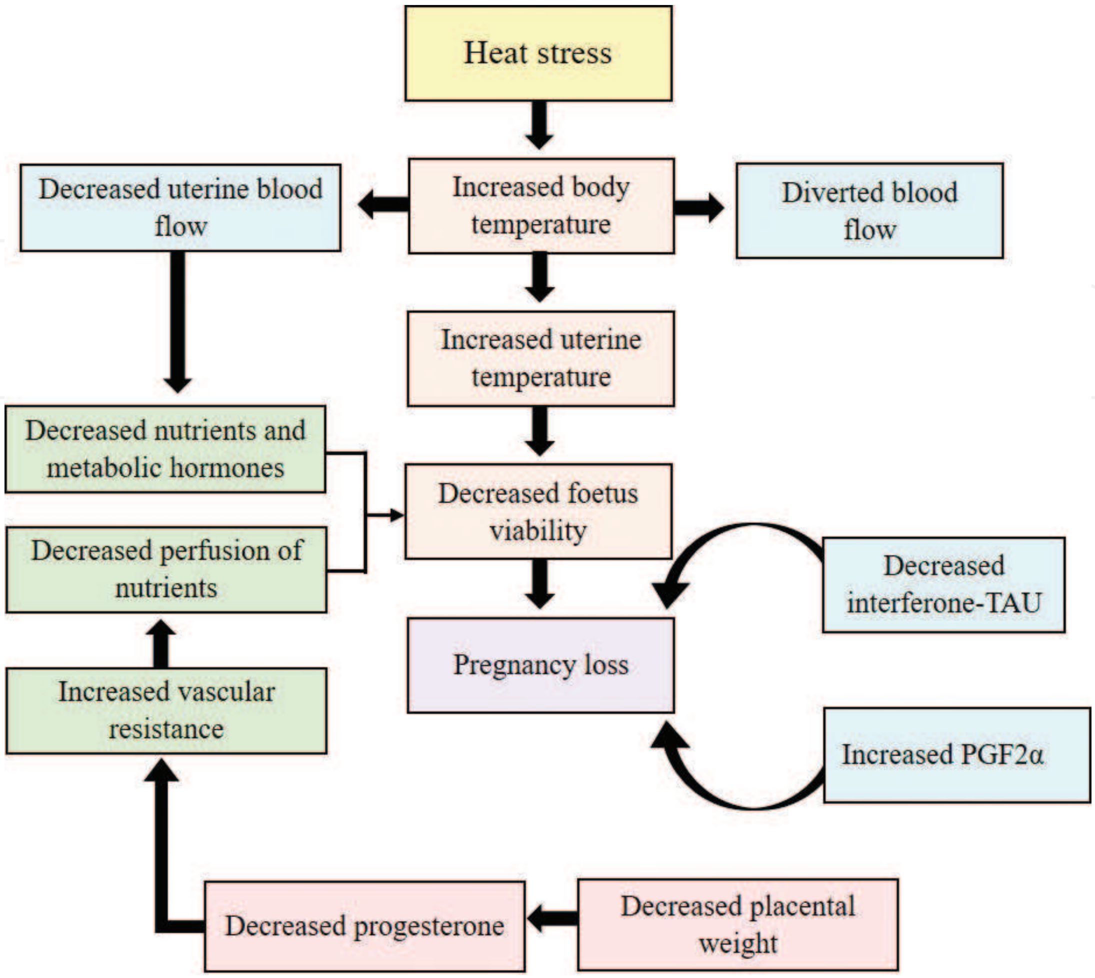

Figure 2. Impact of heat stress on pregnancy in livestock.

3.2% decrease in pregnancy rates in *Bos taurus* cattle for each unit increase in THI above 70, and a decrease of 3.5% for each degree increase in ambient temperature above 23.4°C. Further, heat stress during pregnancy slows down the growth of the foetus, which was attributed to the decreased uterine blood supply [51], which hampers supply of nutrients and hormones to the conceptus [45]. Slow growing embryos fail to signal pregnancy to the maternal organism in due time. Therefore, the endometrial prostaglandin F2alpha (PGF2α) secretion tends to increase during heat stress and trigger luteolysis, thereby threatening the maintenance of pregnancy [29]. Each additional raise of 1.05 unit in the THI over 72, during the peri–implantation period, during 21–30 days and up to 90 days of gestation, increases the chance of pregnancy losses [39]. The placental weight and hormonal secretions are reduced and the vascular resistance is increased during heat stress, which further affects the reduction in perfusion of nutrients to the foetus [23].

2.9. Impact on maternal recognition of pregnancy

The maximum pregnancy losses due to heat stress occur during the early embryonic period of 8–17 days of pregnancy [52, 53]. In addition, heat stress compromises the embryonic growth up to day 17, which was considered a critical period for production of interferon-tau by the embryo. The quantity of interferon-tau is crucial to reduce the pulsatile secretion of PGF2α thus facilitating the persistence of the corpus luteum for the maintenance of pregnancy. Hence, low-quality embryo and poor quality CL are important causes of early embryonic death during heat stress. The heat stress during late gestation period in dairy cows resulted in lower birth weight calves with reduced milk yield, which is associated with a reduced thyroxine, prolactin and growth hormone [54].

2.10. Pre-partum period and days open

The dry period is a critical period, in which the mammary gland involution, the rapid fetal growth and induction of lactation occurs, with subsequent mammary development [36]. Heat stress in the cow impairs the placental hormones secretion, which can negatively affect the intrauterine fetal growth and reduce milk yield [10]. Heat stress in mid to late pregnancy can affect endocrine responses that may increase foetal abortions, shorten the gestation length, lower calf birth weight, and reduce follicular and oocyte maturation in postpartum estrous cycles [55]. Pre-partum heat stress may also decrease thyroid hormones and placental estrogen levels, while increasing non-esterified fatty acid concentrations in blood that alters the growth of the udder and placenta, placental angiogenesis, nutrients supply to the unborn calf and subsequent milk production [10, 54].

The major impact of heat stress on postpartum involves a delay of the return to gestation due to decreased submission rate and low conception/pregnancy rates [55], as already mentioned. Ray et al. [56] reported that first lactation cows are more sensitive to summer stress with the significantly longer postpartum period than cows with multiple lactations. On the other hand, Lewis et al. [57] reported that the heat stress did not alter postpartum days from calving to first estrus, in clear contradiction with Jonsson et al. [58], who suggested that the heat stress induced reduction in dry matter intake may lead to increased negative energy balance, therefore prolonging the postpartum period and reducing the fertility in dairy cows. Further, the negative energy balance decreased the plasma concentrations of insulin and glucose and caused delayed ovulation [33]. The poor folliculogenesis and delayed ovulations during heat stress resulted in longer calving interval, reduced the birth weight and milk yield [51]. Further, longer service period in buffaloes during summer may be due to the higher incidence of silent estrus [1].

3. Male reproductive performance

Bulls are generally considered to be half of the herd and its fertility is directly associated with the fertilization of oocyte to produce a good, viable and genetically potential concepts. In mammalian species, the males have a unique physiological mechanism of testicular thermoregulation to maintain its reproductive activity in adverse environmental conditions [59]. The increased density of sweat glands in the scrotum of ruminants is crucial to the efficiency of local thermoregulation. The testicular temperature in bulls must be 4–5°C below the rectal temperature, and this difference in temperature is essential for an efficient sperm production

[60]. The optimal ambient temperature for efficient sperm production could be approximately 15–20°C. Males are highly susceptible to the pooled effect of high ambient temperature, relative humidity, solar radiation and the wind, and this reduces both the quantity and quality of sperm production, thereby decreasing the male fertility [6, 61] (**Figure 3**). Also, high temperatures interfere with the oxidative metabolism of glucose in spermatic cells as a result of mitochondrial dysfunctions and the accumulation of reactive oxygen species and increase lipid peroxidation which is reflected in an increase of sperm primary defects [62].

The scrotum of bull has thin skin with low fat, low pelage, highly vascularized [59], and its participation in the thermoregulation mechanism is coupled with physical mechanism of counter-current mechanism for heat exchange and blood flow regulation centered in the testicular cord. This complex mechanism allows the maintenance of testicular temperature between 2 and 6°C below body temperature [63]. The local thermoregulation is approbated by relaxation of the dartos (in the scrotum) which together with distension of the cremaster

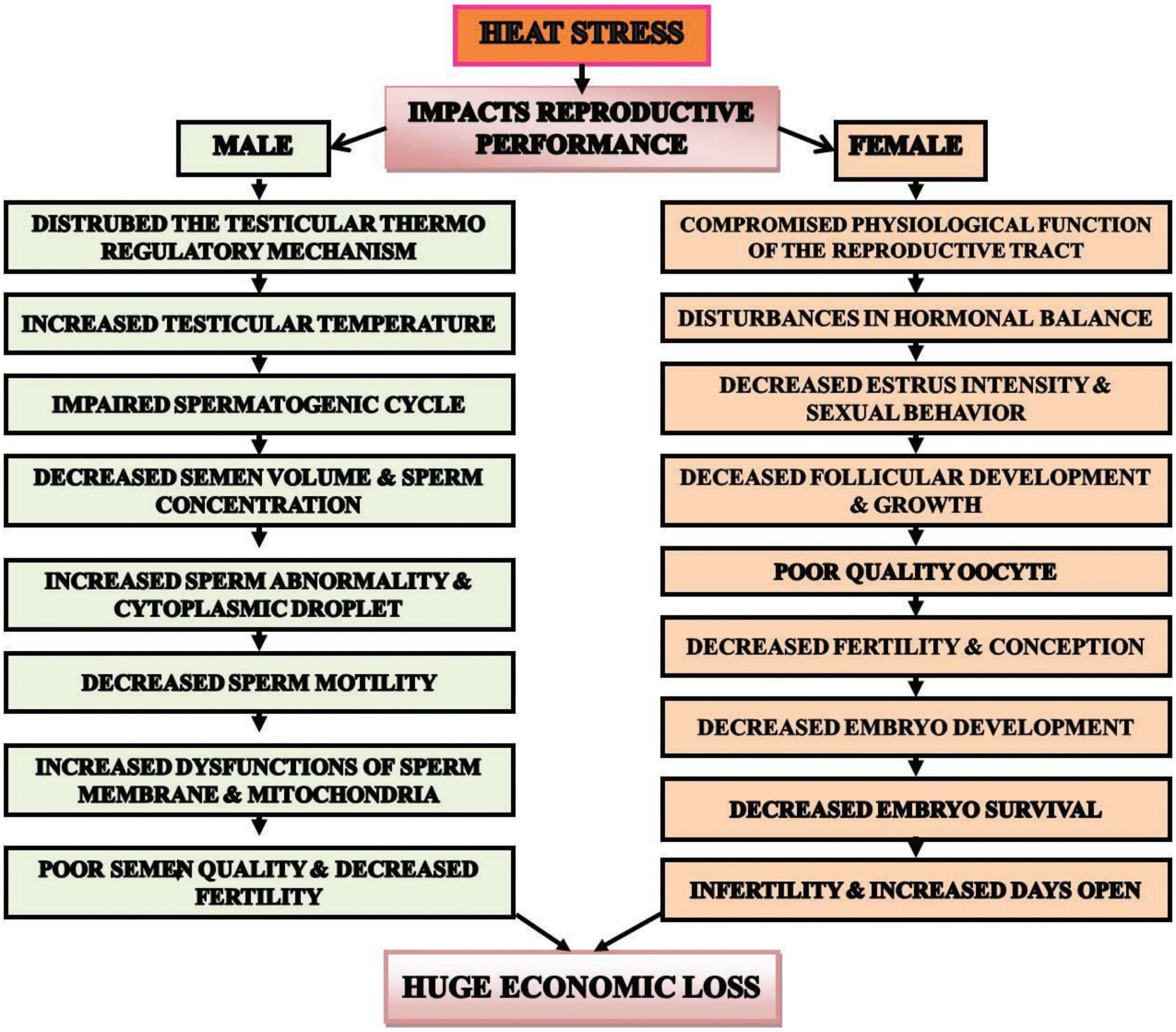

Figure 3. Impact of heat stress on the reproductive performances of livestock.

muscle (in the testicular cord) will increase the distance between the testes and the body cavity [63]. Marai et al. [64] reported that the length of the tunica dartos was greater in summer and autumn than in winter, in rams. Further, it has been established that a high ambient temperature during summer significantly increases the scrotal skin temperature in males. In spite of the efficiency of this mechanism, exposure of the animals to high environmental temperature changes the thermoregulatory mechanisms depending on the thermal gradient and may cause a degeneration of testicular parenchyma which was associated with subfertility and infertility in males, which will negatively impact semen quality and quantity with subsequent reduction in ruminants fertility [63].

The heat stress may also cause a temporary interruption in the semen production, sperm motility and an increase in the sperm secondary defects [65]. Some reports refer that the scrotal skin temperature exhibits highly negative correlation with serum testosterone, libido, sperm motility, sperm concentration and conception rate while it was positively associated with dead and total abnormal sperm [64, 66]. High testicular temperature also results in spermatogonia apoptosis in the seminiferous tubules, degeneration of Sertoli and Leydig cells and disruption of DNA strands, particularly in pachytene spermatocytes and round spermatids [55]. Further, direct exposure of the testes to high temperature also alters the spermatogenic cycle affecting the quality of ejaculate [22]. The changes in libido and sexual behavior in bulls are governed by an imbalance in hypothalamus-hypophyseal-gonadal axis culminating in low testosterone level, sperm output, and motility. In addition, semen attributes like sperm concentration, sperm motility, sperm viability, sperm morphology and acrosome integrity are negatively influenced by heat stress in bulls and bucks, which may ultimately lead to infertility [46, 55].

3.1. Spermatogenesis

The major indicators of sperm production capacity and spermatogenic functions are scrotal circumference and testicular consistency, tone, size and weight that are usually inversely related to higher ambient temperatures. Sahni and Roy [67] reported that the maximum and minimum temperatures for optimum spermatogenesis are 29.4 and 15.6°C, respectively. The elevated temperature hampers the process of spermatogenesis by degeneration of sperm cells and subsequently reduces the fertilizing ability of spermatozoa. Further, seminal characteristics are affected by high temperature and humidity, which affects the spermiogenic phase 18 days before semen collection [68].

Moreover, spermatogenesis is also extremely sensitive to ionizing irradiation and relative humidity above 50% can destroy the proliferating spermatogonia [50]. The analysis of semen obtained from heat stressed bulls showed a reduction in volume and motility along with numerous secondary sperm defects [65]. In addition, the total number of dead and abnormal sperm cells also increased in response to heat stress. The histological sections of testes from heat stressed males showed unchanged or increased interstitium while the spermatogenic elements were seldom found. Further, heat stress was reported to reduce the breeding efficiency in males as the number of testicular cells like secondary spermatocytes and spermatids, the ratio of Sertoli cells to other cells and the diameter of the seminiferous tubules are significantly reduced [35]. Kastelic et al. [69] reported that the minimal temperature gradient between proximal and distal poles of the scrotum in warm periods causes increased sperm damage, mass activity, sperm motility, and vigour. Exposure of the bull to extreme environmental temperature tends to damage the primary spermatocytes, spermatids, and spermatozoa. However, cold stress is likely to be less damaging than higher temperature, and it further was established that the animals during cold stress are able to maintain a scrotal temperature through scrotal thermoregulation [70].

3.2. Semen characteristics

As a consequence of heat stress in males, the biological phenomena such as sexual activity, endocrine secretions and testicular function, spermatogenesis and physical and chemical characteristics of semen are affected. Extremes of environmental temperature may cause low sperm quality, which is closely related to female low fertility, as a result of low fertilization rates and increased embryonic mortality. Abdel-Hafez [71] reported that the reaction time, percentage of sperm abnormalities, dead sperm and acrosomal damage were positively associated with testicular temperature while semen pH, ejaculate volume, sperm motility and sperm concentration ($\times 10^9$ ml) were negatively related. The semen volume, number of spermatozoa and motile sperm cells per ejaculation of bulls are lower in summer than in winter and spring. Nichi et al. [62] reported a higher percentage of major sperm defects during summer than winter in Simmental and Nellore bulls. Conversely, Karagiannidis et al. [72] refer an improvement of semen characteristics of bucks reared in Greece during summer and autumn. The critical temperature for the inhibition of spermatogenesis was established to be around 29.4°C under continuous exposure where the higher temperature can alter the scrotal thermoregulatory mechanism [73].

High temperature can also affect semen production and quality during epididymal maturation or spermatogenesis, not only at the moment of semen collection but up to 70 days before collection. Even though the heat stress has minimal effects on the testicular endocrinology in bulls, the same level of heat stress alters the steroidogenesis in boars [74]. Coulter and Lunstra [75] reported that the percentage of sperm motility was 42% at the temperature gradient of 2–4°C whereas Menegassi et al. [68] reported 53% with a temperature gradient of 0.9°C during summer. The bulls representing an abnormal temperature pattern during heat stress enhanced the percentage of cytoplasmic droplets in sperm cells by 13.4%.

Pigs are very sensitive to hot conditions due to the low sweating capacity. Kunavongkrita et al. [76] reported lower semen volume with less sperm concentration (174×10^6) per mL during summer in comparison with winter (266×10^6) in bulls. The biochemical elements of semen such as fructose, citric acid, and sodium and potassium, total phosphorus and calcium concentration are reduced significantly during heat stress. The semen quality parameters are decreasing with higher lipid peroxidation production as an effect of oxidative stress during summer. The pH of the semen also showed high correlation with environmental temperatures. Further, reduced testosterone concentration was recorded in males exposed to heat stress apart from reducing the reaction time [77].

3.3. Effects of season on semen quality

Sexual behavior, semen quality and quantity are the main factors limiting the male reproductive efficiency in a year. Possible fluctuations in seminal quality are associated with factors such as breed, age, seasonality, temperature, photoperiod and other factors of different etiologies [78]. The month and season of the year show a significant effect on semen quality parameters. The semen output increases when the relative humidity is around 50% and decreases markedly in sperm concentration and total sperm output at temperature of 37°C with 80% relative humidity [79]. The semen volume and sperm concentration are lowest in the summer and gradually increase during the spring and reach a peak in late autumn [78]. Heat stressed bulls produced low quality semen with high number of abnormal heads and cytoplasmic droplets during summer [80]. The seasonal infertility in rams during summer months was attributed to an early occurrence of the acrosome reaction, which could be due to a decreased in acrosomal stabilizing protein in the seminal plasma [55].

4. Mitigation strategies to ameliorate the impact of heat stress

The effects of heat stress on livestock cause huge economic losses to the farmers, but there are few opportunities to recover some of the losses by adapting suitable strategies to mitigate heat stress (**Figure 3**). There are three major key components to sustain the productivity of animals in hot environment: through physical modifications of environment, nutritional management and genetic development of breeds that are less sensitive to heat stress [5]. These strategies may either be used individually or in combination to obtain better results by providing optimum productive environment for farm animals. In addition, summer infertility may also be treated with advanced reproductive technologies comprising gonadotropins, timed artificial insemination and embryo transfer. Strategies that are cost effective and involve indigenous knowledge have the better success rate in adopting those strategies by the farmers.

4.1. Physical modification of environment

In general, livestock environmental management is an emerging area in animal science, which is getting more attention in the era of climatic change, attempting to provide a suitable microclimate to ensure optimum production by preventing the adverse environmental impacts on animal production systems. Primary means of altering the environment may be broadly divided into two categories comprising (i) provision of shade and (ii) evaporative cooling techniques [6]. The environmental modifications such as shade and cooling systems are critical in arid and semi-arid zones during heat stress to maintain milk production, milk component levels, reproductive performance and animal welfare [81]. The basics of providing shade are attributed to the efforts in reducing heat load from direct solar irradiation in livestock. These shading structures could be either natural or artificial. Trees are considered to be the most cost effective methodology to provide shade since they protect from the sun and capture radiation by evaporation of humidity in the leaves. Buffington et al. [82] pointed out that painting of upper part of the shade unit with white color and installing a 2.5 cm thick of isolating material may considerably reduce solar radiation. The height of shades in the corral must be from 3.6 to 4.2 m in order to guarantee reduction in solar radiation. It has been established that shading reduces the incoming radiant heat load by 30% or more and shading of the feed and water also offered production advantages for British and European breeds of cattle [83]. The cooling systems alleviate heat load from livestock by using the principle of evaporation, combining water misting and forced ventilation through use of spray and fans, and are frequently placed inside free-stall barns or under shades in open space corrals. Milk production and reproductive performance of dairy cattle are improved by the use of an evaporative cooling system [84]. Furthermore, the animals that are cooled with sprinklers consume more feed with less quantity of water, which has increased milk, fat, protein and production performance [85]. Fogging and misting systems use fine droplets of water, which are immediately dispersed into the air stream by quick evaporation and cool the surrounding environment.

4.2. Nutritional management of heat stress

Ensuring appropriate nutritional level to the livestock is crucial to optimize livestock production in the changing climatic condition. Importance should be given for providing balanced nutrition to ensure optimum reproduction in animals as the energy balance are closely associated with their fertility [86]. The environmental temperatures are highest in arid and semi-arid regions where the available feed resources are both of low quality and quantity which directly affect the reproductive performance of the livestock species. Combating the heat stress effects on the metabolism is therefore very essential, as animals subjected to mild to severe heat stress needs to be supplemented 7–25% extra maintenance requirements [87]. Therefore, to meet their energy requirements, it is essential to enhance the nutrient density by feeding high quality forage, concentrates and fat supplementations. In addition to the supplementation of low fiber, high protein diet was also found to be helpful by reducing the water requirement for metabolism. Feeding of feed additives stabilizes the distorted rumen environment and also improves the energy utilization [88]. Moreover, fat content in the diet has favorable effects on concentrations of cholesterol, progesterone, rate of synthesis and metabolism of PGF2 α, follicle growth and pregnancy rates in dairy herds [89]. Also, dietary supplements of vitamins, trace elements and minerals can ameliorate the adverse effects of heat stress. Vitamin E and selenium injections reduce the rectal temperature and body weight loss in sheep during summer [19]. Supplementation of inorganic chromium in the feed of buffalo calves reared under high ambient temperature improved heat tolerance and the animal immune status without affecting nutrient intake and growth performance. It was also demonstrated that the adverse effect of heat stress on the productive and reproductive efficiency of Malpura ewes were reversed through mineral mixture and antioxidant supplementation [19]. DiGiacomo et al. [90] also reported that the feeding of betaine, a trimethyl form of glycine, ameliorate heat stress in sheep. Feeding buffers during heat stress is highly beneficial to animals, since buffers assist in the prevention of low rumen pH and rumen acidosis [91]. Also, the addition of common macro minerals Na^+ and K^+ in feed increases dry matter intake and production performance [91]. Inclusion of ascorbic acid in the feed ameliorates, heat stress induced problems like poor immunity, feed intake, weight gain, oxidative stress, body temperature, fertility and semen quality [92]. In addition, supplementation of L-ascorbic acid, both singly and in combination with l-tocopherol acetate, was found to be helpful to heat-stressed layers [92].

4.3. Genetic selection of heat-tolerant breeds

Scientific advances allow improving the environmental modifications and nutritional management in the view of alleviating the impacts of thermal stress on animal performance. However, long-term strategies are foreseen for adaptation to climate change, namely regarding the differences in thermal tolerance existing between livestock breeds, endowed with tools to select thermo-tolerant animals. However, the selective breeding of dairy cows for higher milk production has increased the susceptibility of cows to heat stress by compromising the summer production and reproduction. Furthermore, selection for high milk yield reduced the thermoregulatory range of the dairy cow and resulted in heat stress which has magnified the seasonal depression in fertility [15]. Hence, the identification of heat-tolerant animals within high-producing breeds will be useful only if these animals are able to maintain high productivity and survivability when exposed to heat stress conditions. Cattle with shorter hair, hair of greater diameter and lighter coat color are more adapted to hot environments than those with longer hair coats and darker colors [93]. This phenotype has been characterized in *B. taurus* in tropical environment, and this dominant gene is associated with an increased sweating rate, lower rectal temperature and lower respiratory rate in homozygous cattle under hot conditions [94]. The heat shock protein genes that are associated with thermo-tolerance have been used as markers in the marker-assisted selection breeding program. The association of polymorphisms in heat tolerant genes is reported in various breeds such as HSP90AB1, in Thai native cattle [95], or the HSF1 gene, HSP70 A1 A gene and HSBP1 in Chinese Holstein cattle [96, 97]. In addition to HSPs, there are also other thermo-tolerant genes reported in ruminant livestock species which undergo changes in their expression pattern while subjecting them to heat stress. The other genes of economic importance include ATP1B2, thyroid hormone receptor, interleukins, fibroblast growth factor, protein kinase C, NADH dehydrogenase, phosphofructokinase and glycosyl transferase, among others [6, 97]. However, further detailed studies are required to elucidate the expression pattern of these genes in diversified animal species before they may be considered as biological markers to be used in marker assisted selection program to develop thermo-tolerant breeds, which can produce and reproduce normally.

4.4. Hormonal treatment and assisted reproductive technologies

Hormonal treatments have the potential to minimize the heat stress effects in animals. The administration of GnRH in the early stages of estrus coincides with the endogenous LH surge and improves the conception rate successfully. GnRH agonist or hCG injected on day 5 of the estrous cycle results in ovulation or luteinization of the first wave dominant follicle and forms an accessory corpus luteum (CL) that enhances the plasma progesterone levels to compensate its decrease in chronic heat stress [2, 98]. The timed artificial insemination (AI) program also improves summer fertility when associated with an injection of GnRH to induce a programmed recruitment of the ovulatory follicle. This protocol should be followed by PGF2α injection 7 days later to regress the CL which permits the final maturation of ovulatory follicles. Further, a second dose of GnRH 48 h after PGF2α may induce ovulation and the insemination of cows at 16 h to ensure successful conception [99]. The Ovsynch protocol successfully synchronized the ovulation in buffaloes and increased conception rate when combined with timed AI [100]. El-Tarabany and El-Tarabany [101] reported that the CIDRsynch and Presynch protocols improved the conception and pregnancy rate of Holstein cows under subtropical environmental conditions. Embryo transfer (ET) improves pregnancy rates during summer because embryos are transferred after the time at which they are more sensitive to heat stress. Compared to AI, pregnancy rates in cows exposed to heat stress have been improved by transfer of either frozen or unfrozen embryos produced by superovulation [102].

5. Conclusion

Under the climate change scenario, elevated temperature and relative humidity will definitely impose heat stress on all the species of livestock and will adversely affect their reproductive ability. This chapter discussed in detail the impact of heat stress on both female and male reproductive performance. This chapter also elaborated on ameliorative strategies that should be given consideration to prevent economic losses incurred due to environmental stresses on livestock reproduction. Fortunately, proven strategies exist to mitigate some effects of heat stress on animal reproduction. These include housing animals in facilities that minimize heat stress, use of timed AI protocols to overcome poor estrus detection and implementation of embryo transfer programs to bypass damage to the oocyte and early embryo caused by heat stress. Management alternatives, such as the strategic use of shade, wind protection, sprinklers and ventilation in the summer, also need to be considered to help livestock cope with adverse conditions. In addition to these measures, manipulation of diet energy density and intake may also be beneficial for livestock challenged by environmental conditions. There are also several promising avenues of research that may yield new approaches for enhancing reproduction during heat stress. These include administration of antioxidants and manipulation of the growth axis. Opportunities also exist for manipulating animal genetics to develop an animal that is more resistant to heat stress. Genes in animals exist for regulation of body temperature and for cellular resistance to elevated temperature and identification and incorporation of these genes into heat sensitive breeds in a manner that does not reduce production and reproduction would represent an important achievement.

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