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Influence of Seasonality on Mammals Reproduction

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Review Article

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INTRODUCTION

Reproduction is the most important biological activity for any animal population, since it is responsible for the origin of the individuals of the next generation, and it ensures the survival of the species. It multiplies the herds' activities for commercial breeding and generates an interface with selection and genetic enhancement work in research [1,2]. The reproductive management covers several aspects, such as feeding, mating system, the use of biotechnology for genetic improvement, establishment of criteria for the selection of breeders and matrices, and reproductive disease control[3].

The reproductive activity can be affected by several factors such as the influence of climate and its changes, which are decisive for the semen quality in several species[2,4-7]. Similarly, in females, exposure to stressors such as high temperatures, food, and water deprivation can act on the hypothalamic-pituitary-gonadal axis, jeopardizing their operation[8]. These factors reduce the release of gonadotropin-releasing hormone (GnRH) from the hypothalamus and determine a decrease in the frequency and amplitude of luteinizing hormone (LH) released from the pituitary gland, resulting in abnormal ovarian function due to the non-occurrence of LH surge and thus inhibiting follicular development and ovulation[8,9].

In this context, the reproductive seasonality consists of the phenomenon by which some species have reduced sexual activity during a certain period of the year, mainly regulated by climatic factors such as temperature, air humidity, or photoperiod[4,5,10]. In tropical climates, high ambient temperature observed in the dry season is one of the main limiting factors for reproductive efficiency, and may affect testicular thermoregulation, interfering in the process of spermatogenesis and semen quality[11-14]. These characteristics, combined with the production of forage of poor nutritive value, require that the animals exhibit heat tolerance, skill conversion of roughage, and resistance to parasites, once the animal productivity depends of its degree of adaptation to the environment and their interactions[15]. Thus, reproduction is the most positive evidence of animals being able to adapt to a particular environment[16]. The reproductive performance is the main phenomenon responsible for the success of production, being fundamentally dependent on the genotype and environment[17].

This study aimed at conducting a review on the influence of climatic aspects, such as photoperiod, temperature, rainfall regimes, and food availability that may interfere with a mammal's reproduction.

Physiological mechanisms

Many mammalian species have various physiological mechanisms for maintaining their reproductive activity in the face of environmental adversity, among which testicular thermoregulation stands out. Among the different thermoregulation processes, the positioning of the testicles within the scrotum consists of a process derived from the evolution of most terrestrial mammals, which is based on the placement of this organ in the area outside of the male body, with the purpose of maintenance of a distinct temperature level in the rest of the body[18]. In addition, the nature of the scrotum, with thin skin, low fat, and low pelage, highly vascularized, coupled with physical mechanisms such as countercurrent heat exchange, blood flow regulation, the position of the testicles, and sweating, plays an important role in the maintenance of testicular temperature 2 ° C to 6 ° C below body temperature[19]. However, exposure of the animals to high environmental temperatures changes the thermoregulatory mechanisms, which may cause, depending on the thermal gradient, a degeneration of the testicular parenchyma, which is the main cause of subfertility and infertility in males[20].

Studies conducted in several species have shown that the degeneration of gonadal germinal epithelium leads to a reduced semen quality, which is reflected in the increase in sperm pathology, and reduced motility and sperm vigor[21,22]. This is due to impaired spermatogenesis, especially in the intermediate phase (spermatocytes and spermatids), and changes in the epididymal epithelium[23-25].

In females, the control of gonadotropin secretion during the estrous cycle requires a delicate balance between the complex hormonal interactions. Hypothalamic nuclei secretes GnRH, which through the hypothalamic-pituitary portal system stimulates the anterior pituitary to secrete LH and follicle-stimulating hormone (FSH), thus promoting the synthesis of estrogen and progesterone by the ovaries[26]. These latter two exert influences by positive or negative feedback mechanisms, directly on the pituitary or hypothalamus, making possible the continuity of the cyclic events that characterize the estrous cycle[26,27]. That cycle is determined by the pace of functional female reproductive organs that are established from puberty, comprising cyclic changes in the physiology and morphology of the genital organs and also in the related hormone profile[28,29].

In goats bred in tropical regions, the period of seasonal anestrus varies in intensity and duration depending on the latitude, race, lineage within the same race, the climate, and genetic and social factors. In addition, it can be influenced by the stage of lactation and management practices, such as the animal feeding. The nutritional deficiency is among the main factors that can interfere with reproduction of females created in this tropical regions, since the energetic support is usually not enough to maintain the production processes in the dry period[30,31].

Once the acclimatization to a high temperature environment involves processes that lead to the reduction of the thermal load, the immediate response is the reduction in food intake, increase in respiration rate and water intake, and changes in hormone levels that affect the responsiveness of the target tissue to environmental stimuli[32]. If the exposure to high temperatures is extended, the lower feed intake is followed by a decline in the secretion of hormones, such as growth, catecholamines, and glucocorticoids, as well as by thermogenic processes of digestion and metabolism, thereby reducing the production metabolic energy to be used in maintenance processes, production, and animal breeding[33].

Additionally, harsh environmental conditions and risk of predation and malnutrition are the most relevant stressors for free-living vertebrates[34]. The activation of the hypothalamic-pituitary-adrenal axis by stress generates a cascade of hormonal messages that culminate in increased concentrations of plasmatic cortisol, which in turn inhibits the activity of hypothalamus and pituitary gland, producing negative effects on animal reproduction[35,36].

Influence of photoperiod

The photoperiod is the duration period of light of a certain place, depending on the latitude and season, and is represented by the length of a day. The ability of animals to react to the duration of daily light that they are subjected to is called “photoperiodism.” In seasonal animals, variations in the annual reproductive cycle occur due to changes in day length and melatonin secretion profile, thus being classified as the negative or positive photoperiod for animals[5,37].

In horses, animals that are long-day seasonal or positive photoperiod, the increased exposure of melatonin has the opposite effect, inhibiting the secretion of GnRH by the hypothalamus and, consequently, reducing the production and release of LH by the anterior pituitary. Thus, in the Southern Hemisphere, the period of greatest brightness is the most favorable season for breeding[38,39]. In addition, the domestic cat also behaves similar to a long-day animal, once the sperm production provides evidence of being influenced by the photoperiod, thus becoming greater with an increasing exposure to sunlight[40].

In sheep and goats, the influence of this phenomenon is striking in both male and female breeds coming from the northern hemisphere, which begins their annual reproductive cycle due to the decrease in the intensity of light daily, thus being considered animals presenting a negative photoperiod[41]. Thus, in the dark, the pineal gland synthesizes and secretes melatonin, which stimulates the hypothalamus, the pituitary gland, and the ovaries or testes to the return of the reproductive activity[31,42]. Buffalo (Bubalus bubalis) also behaves similar to a short-day seasonal poliestral animal (negative photoperiod) or as a continuous poliestral animal depending on the proximity to the Equator[2,43].

Most wild ruminants as the Alpine ibex (Capra ibex), the Iberian ibex (Capra pyrenaica) and the mountain goat (Oreamus americanus) present a short breeding season, usually from November to February, and the photoperiod is the main environmental

cue regulating seasonal breeding activity in these species[5,13]. Santiago-Moreno et al.[14] also reports that testicular activity and secondary sexual characteristics development can be changed by manipulating the photoperiod. The male goral (Naemorhedus griseus) of the Thailand showed seasonal variation in testicular and adrenal steroidogenic function, with greater activity in the rainy season and winter. Given that resources for this animal are consistent throughout the year, reproduction may be primarily regulated by photoperiod in this species[44]. Camels are also considered seasonal breeders, under the influence of the photoperiod; however, when these animals are raised near the equator, factors such as rainfall, nutrition, and management may override the effects of photoperiod and allow breeding to occur throughout the year[45].

Therefore, in regions where there is not much differentiation in the length of days and nights, the animals suffer less due to the effect of this phenomenon, with the reproductive seasonality being more related to thermal stress, nutritional deficiencies, health, and the husbandry system[28,46].

Influence of thermal stress

The intensity of solar radiation directly affects the behavior and physiology of domestic animals and determines their adaptability to the environment. Mammals adjust their physical, biochemical, and behavioral processes in an attempt to contain the negative effects of thermal stress, which involves heat dissipation to the environment and reduces the production of endogenous heat, reflecting the restriction of reproductive activity[47-50].

Mathevon et al.[51] reported that the concentration of semen, under temperate conditions, and the number of sperm and mobile cells ejaculated by bulls are lower in summer than in winter and spring. In regions where the predominant climate type is hot and humid, the increase of the temperature and humidity index (THI) ranging from 63.9 to 82.6 enables the respiratory rate and skin temperature to rise in the female buffalo, whereas there is a decrease in sweat rate and consequently a decrease in the loss of body heat, causing thermal stress[52]. In addition, Garcia[2] states that this phenomenon can adversely affect the reproductive physiology of buffaloes, generating a change in reproductive behavior, reducing the manifestation of estrus and conception rates, and causing a decline in pregnancy maintainability, which reduces fertility. The male buffaloes subjected to the same weather conditions have reduced sperm quality and changes in semen composition[2]. In horses, normal intratesticular spermatogenesis occurs at a temperature of 35°C on average, and most of the testicular problems of stallions are related to changes in their ability to control testicular temperature[53].

Under semiarid climate, Nunes et al.[54] reported that the male goat may present a certain seasonal production that depends on a series of intrinsic variables such as race, weight, and age; extrinsic variables such as latitude, temperature, and power. In sheep, the seminal characteristics most affected by high temperatures are motility, vigor, concentration, and morphology[16]. Maia et al.[4] attributed the high percentage of sperm morphology damage observed in Dorper and Santa Inês sheep to the negative effect of ambient temperature on spermatogenesis and sperm maturation, since the samples were collected in the summer, high-temperature environment period. As a result, rectal temperature was elevated to approximate values of 39°C to 39.5°C, resulting in the appearance of abnormal spermatozoa in the ejaculate, especially with tail pathologies, isolated heads, and cytoplasmic droplets, with these types of defects directly related to thermal stress[4].

Pigs are very sensitive to hot conditions, mainly due to the low capacity of the species to heat loss. In feral pigs, Macchi et al.[55] evaluated the reproductive seasonality in two northeastern areas of Italy: one in alpine climate, characterized by coniferous forest, and the other in a plain, grazing area, experiencing a warm climate. The authors identified the existence of different patterns of reproductive rates between the two geographically distinct populations created in these regions because of, among other factors, the various environmental conditions. Studying peccaries (Pecari tajacu) in captivity, Hellgren[56] determined that the highest testosterone concentrations occurred between the months of October and March, coinciding with the time of the highest number of species mating in southern Texas, USA. In addition, the authors described the relationship between the circulating levels of the hormone with the season and ambient temperature, suggesting a reduction in the reproductive performance of males during late summer, due to the occurrence of high temperatures[56].

Influence of rainfall regime and food availability

In the semiarid region, as well as due to direct climate action, animals suffer from the poor quality of food that is almost exclusive pastures produced in low fertility soils, which is the result of intense leaching that causes forage production irregularity[15,4]. In addition, there is the effect of seasonality of rainfall and other weather conditions that do not allow uniform production throughout the year, with excess in the rainy season and shortages in the dry season and the low digestibility of forage due to the low protein content and high fiber[33,57]. Low[58] proposed that the high ambient temperature or nutritional stress induced by drought or protein forage decreases during the late summer, can reduce male reproductive activity reflecting acyclicity females, since nutritional factors are important for both the establishment of puberty and the maintenance of ovarian cyclicity, resumption of cyclicity postpartum, and maintenance of pregnancy in buffaloes[2].

According to Cavalcante et al.[59] changes in semen characteristics and libido of sheep and goats of different breeds are due to variations in climate, as evidenced by studies that described the influence of light, temperature, and rainfall in breeding animals. So, in some tropical or subtropical regions, the goats can behave similar to continuous polyestrous, with the nutrition

and health status being among the main factors that can interfere with reproduction[60,61]. Thus, the effect of season on the quality of the different breeds of sheep semen has been the subject of several studies[62] in which wooless races have generally well adapted to the region, suffering due to less influence of climatic factors on semen quality[4]. However, in Santa Inês and Somalis sheep, the time of year affected the volume and sperm concentration, with a larger volume and a lower concentration in the rainy season[63]. In addition, in the rainy season, we observed a significant increase in mass motility and sperm concentration in semen of the same kind in the Santa Ines breed, otherwise observed in the dry season, when there was impaired spermatogenesis, whose disability substrates for energy production resulted in nutritional deficiency of animals[64].

Similar studies were carried out by Coimbra[65] under humid tropic weather while evaluating seminal characteristics of zebu semen donors, taurine, and buffaloes that were kept in an artificial insemination center in the state of Pará. The author analyzed ejaculations collected during the most rainy season (January to June) and during the less rainy season (July to December); the results showed that the buffalo bulls showed differences in semen quality, which was always favorable to ejaculate produced in the rainy season of the year. Sperm motility was the attribute that showed greater differences in both the semen in natura as post freezing. In addition, Garcia[2] reported that nutrition in the same species is an important element and where deficit, it reduces the body condition of the animals, with negative impacts on the age at puberty, the age at first calving, and calving interval. In cattle, the reduction in energy consumption due to poor intake of food results in a negative energy balance, and it partly explains why the cows lose significant amounts of weight and body condition when subjected to thermal stress and nutritional deficiency[66].

Regarding wildlife, Dubost et al.[67] investigated the reproductive seasonality of three species of rodents in the rainforest of French Guiana: the Myoprocta exilis, the Dasyprocta leporina, and Agouti paca. The authors concluded that Myoprocta exilis showed the most evident features of seasonality, with 56% of births concentrated between the months of November and January; the Dasyprocta leporina also performed seasonally, but to a lesser extent; and the Agouti paca apparently produced during most of the year. The authors attributed this to the seasonality in the production of some fruits of the forest, which were important in the diet of these animals, and also reported that less seasonal species had a more diverse diet for the poorest season of these fruits. However, under the conditions of the humid tropical Amazon, the agouti presented a continuous reproduction being classified as poliestric, both in captivity and in the wild[68]. However, it is noteworthy that Weir[69] reported that one reproductive seasonality period occurs in captivity for this species in temperate conditions.

Trillmich et al.[70] showed that in guinea pigs (Cavia aperea) the photoperiod is an important factor in determining the reproductive seasonality of the species, whereas Bauer et al.[71] stated that the seasonal level varies with nutritional components such as proteins, which are essential for perinatal development of this kind.

In desert, where unpredictable rainfall arises and a large variation in temperature occurs, severe energetic and water related constraints influence the native small mammals reproduction. The harsh conditions associated with arid environments can constrain reproduction in rodents to the favorable period which maximizes the growth and survival of offspring[72]. Sarli et al.[6] reported that the Acomys imidiatus placed in arid region of Saudi Arabia reproduces seasonally with the cessation of reproduction during winter. This appears to be tightly linked to the rainfall and indirectly to other factors as the salinity in the desert vegetation that serves as food for such animals.

The hairy nose wombat (Lasiorhinus latifrons) breeding occurs between July and December (winter and spring) and is highly dependent of annual rainfall and the nutritional content of vegetation with cause changes in semen quality, plasma testosterone secretion and bulbourethral size[7].

In collared peccary, Lochmiller et al.[73] reported decreased serum levels of testosterone and scrotal circumference after nine weeks followed by nutritional deficiency. Hellgren[56], in turn, determined that the concentration of this hormone in peccaries did not vary significantly by season, but seasonal values were higher in winter (February–March). In addition, testicular volume and scrotal circumference in captive animals varied significantly, with higher measures between late October and late February for both traits. However, smaller amounts were recorded in the summer months, also noting that the average monthly scrotal perimeter ranged from 182 ± 12 mm in September to 228 ± 8 mm in January[56].

While studying peccaries created in eastern Amazonia, Kahwage et al.[74] observed fluctuations in seminal parameters of ejaculates over a year. In this study, the authors demonstrated a reduction in the values for semen parameters, especially between the months of March and May, with reduced motility and plasma membrane integrity and a concomitant increase in total sperm defects. As for animals of the same species maintained in semiarid climate, conditions have not yet been developed for long-term studies and under the environmental conditions monitored.

With regard to the reproduction of marine mammals, environmental, nutritional or social influences may affect the oestrus cycle, thus affecting the reproductive season[75]. For example, the values for serum testosterone in mature male killer whale (Orcinus orca) (>13 years) demonstrated periods of elevation from spring to fall. Despite these apparent seasonal rhythms in testosterone secretion (particularly within each animal), sperm production did not exhibit an obvious seasonal change with conceptions occurring throughout the year[76].

Regarding social influences on reproduction, some researchers say non-human primates differed from all other mammals

since its sexual activity occur without interruption throughout the year. On the other hand, many other primates mate seasonally and in the rest of the year display a complete cessation of true copulation. In fact, a discrete reproductive period may be thought to allow gestation, births and early development to occur when the environmental conditions are most favorable. A growing body of evidence confirming that many primate species, if not completely seasonal, do at least tend to indulge in sexual activity more often at one time of the year than another[77]. Although ecological factors are undoubtedly important in timing seasonal transitions, there is considerable evidence in squirrel monkeys and other seasonally breeding animals that the coordination of reproductive changes between individuals is mediated by social stimulation[78,79]. Schiml et al. [78] evaluating seasonality in Squirrel Monkeys (Saimiri sciureus) found that the distribution of births was highly seasonal. The initial birth peak (November-December, 1989) followed group formation by 6-7 months. Estimates of the timing of conceptions indicated that the first breeding season included the months February through June, 1990, and the second breeding season commenced in February and ended in May, 1991, when behavioral and endocrine data collection ended. In wild Cebus apella the birth periods occur during the early to mid-wet season, both at this site, and elsewhere throughout their geographic range[80,81]. In direct contrast, plasma testosterone levels in captive Cebus apella show no circannual rhythm, and births in captivity may occur throughout the years[82].

CONCLUSION

From what has been mentioned earlier, it can be inferred that animals subjected to semiarid climate suffer little or no interference from the photoperiod. However, the factors related to thermal stress and poor food availability caused by erratic rainfall can reduce the reproductive capacity of these animals, thus creating a period of reproductive seasonality in some species during the months of higher and lower temperature availability of fodder in the dry season (July to December). Some steps that can be taken to minimize the negative effects of climatic aspects on animal reproduction are deploying shading areas in pastures, or heat dissipation mechanisms in plants and even nutritional supplementation, which can be realized through conservation techniques, forage such as silage or hay, and grazing areas when conditions permit water availability, according to each breeding system.

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