Uludag Univ. J. Fac. Vet. Med.
30 (2011), 1: 73-82

Physiological Mechanisms of Multiple Ovulations and Factors Affecting Twin Calving Rates in Cattle

Özden ÇOBANOĞLU[1]

Geliş Tarihi: 04.04.2011
Kabul Tarihi: 09.05.2011

Abstract: Reproduction in bovine is affected by several different factors. These factors explain some of the variations observed in the reproductive efficiency of animals. Several comprehensive studies were conducted to assess the incidence of twinning at birth in various dairy and beef cattle breeds. In this manner, many environmental and genetic factors affecting reproductive system have been studied quite extensively. Even if the natural incidence of multiple births in cattle is very low, some variations on the twinning rate can be observed due to the influence of breed differences, the effects of feeding and management systems and also the effects of some environmental sources such as a parity, an age of cow, a season of the year and a geographic location of raised animals. Thus, the main purpose of this review is to emphasize and explain the physiological mechanisms regulating multiple ovulations in cattle and also some of the important factors affecting multiple births positively or negatively on the cow production system.

Key Words: Double ovulations, follicular development, twin calving, risk factors, parity and seasonal effect, breed difference.

Çoklu Ovulasyonların Fizyolojik Mekanizmaları ve Sığırlarda İkiz Yavru Oranlarını Etkileyen Faktörler

Özet: Büyük baş hayvanlarda üreme çok çeşitli faktörlerden etkilenmektedir. Bu faktörler hayvanların üreme performansında gözlenen bazı varyasyonu açıklar niteliktedir. Doğumda ikizlik görülme sıklığını değerlendirmek için kapsamlı birçok çalışma, süt ve et ırkı büyükbaş hayvanlarda yapılmıştır. Bu anlamda, sığırlarda üreme sistemi üzerine etkili pek çok çevresel ve genetik faktörler oldukça geniş bir şekilde ele alınmıştır. Sığırlarda çoklu doğumun görülme oranı çok düşük olsa bile, ırk farklılıkları, besleme ve yönetim sistemleri ve bunun yanında doğum sırası, ana yaşı, yılın mevsimi ve yetiştirilen hayvanın coğrafik konumu gibi değişik çevre faktörleri de ikiz doğum oranı üzerine etkili bazı varyasyonun görülmesine neden olabilmektedir. Dolayısıyla, bu derlemenin amacı sığırlarda çoklu ovulasyonu düzenleyen fizyolojik mekanizmayı ve aynı zamanda büyükbaş hayvan yetiştiriciliğinde çoklu doğumu olumlu ya da olumsuz yönde etkileyen bazı önemli faktörleri vurgulamak ve açıklamaktır.

Anahtar Kelimeler: Çift ovulasyon, foliküler gelişim, ikiz buzağılama, risk faktörleri, doğum sırası ve mevsimsel etkiler, ırk farklılığı.

[1] Uludag University, Faculty of Veterinary Medicine, Department of Genetics, Bursa, ocobanoglu@uludag.edu.tr

Introduction

Reproductive performance of cattle is a major determinant for efficient meat and milk production. Therefore, the reproduction of animals greatly influences net income of the beef producers in a cow-calf operation. However, the reproductive performance of cows will necessitate a better understanding of the physiological mechanisms and also environmental effects controlling the developmental processes of the ovarian follicle, a gestation period after fertilization and a calving performance of cows in post-natal period. In this review, the physiological mechanisms of multiple ovulations especially for double ovulation cases and mainly the breed differences and some of the environmental factors influencing twin births significantly in cattle breeding were discussed in details.

Physiological Mechanisms of Twinning

Dynamics of Follicular Growth

Cattle are primarily a monotocous species which are able to produce a few hundred thousand primordial follicles at the beginning of puberty. However, practically less than 1% of these follicles will grow and be ovulatory in late stages of development due to atresia. Folliculogenesis, which is the complex process of forming ovulatory follicles among the group of primordial follicles on the ovaries, causes the changes in morphological characteristics of the ovary during the normal estrus cycle. Rajakoski proposed the first model in which the ovarian follicular growth in cattle takes place in a wave-like pattern[43]. Many researchers reported that each cycle usually involves two or three waves[54]. Application of transrectal ultrasound technology has facilitated understanding of the pattern of follicular waves during the estrous cycle. Firstly, Pierson and Ginther observed individual follicular development during the cycle by using this technology[42]. After that, several studies were conducted to investigate these developmental stages of the cycle in farm animals, especially intensive studies in sheep and cattle breeds[4,29]. Specifically, primiparous and multiparous dairy cows display a two-wave cycle most of the time, in contrast to nulliparous dairy heifers, 2-2.5 years of age, which have three-wave cycles. After puberty, all of the primordial follicles have equal opportunity to become a mature follicle. But one of them is eventually selected to be dominant and thereby capable of becoming ovulatory among the group of follicles within each follicular wave[48]. All of the others unfortunately will degenerate during the normal estrous cycle. Studies proving that the developmental processes of follicles within a follicular wave are highly variable among waves were observed by Wiltbank and his colleagues[59]. In general, follicles are categorized as dominant and subordinate. The follicle that has the largest size in diameter is typically the dominant or mature follicle of the wave and the subordinate follicles are ones that belonged to the same group of follicles from which the dominant follicle came from[27]. The day when a follicular wave is first detectable determines the day when an initial observation of the dominant follicle can be made retrospectively[16].

A first follicular wave emerges when the follicles are 4-5 mm in diameter at approximately the day of ovulation. Subsequently, a second ovulatory wave can be detected about 9 or 10 days later[15]. But a high progesterone concentration prevents the first dominant follicle to continue for becoming a mature one since the corpus luteum has not regressed yet. Thus, the first dominant follicle cannot be functional and ovulatory. Subsequently, a second ovulatory wave can be observed. The dominant follicle from this wave is able to continue for growing and ovulating during the time of corpora lutea (CL) regression. In addition, a third source of the ovulatory follicle becomes apparent on day 16 after ovulation in some cattle due to the regression of the second dominant follicle during luteolysis. Even if each wave contains simultaneous emergence of a cohort of follicles, usually one of them, sometimes two, become dominant follicle(s) and all of the others ultimately become subordinates. A single oocyte is released from the dominant follicle due to either naturally occurring or artificially induced ovulations. On the other hand, subordinate follicles begin to regress after a short growing phase[15,16].

From individual to individual, it was realized that the size of follicles at the time of ovulation is highly different. Dairy heifers that show two-wave cycles have a follicle at the diameter of 16.5 mm in ovulation. However, follicle size is smaller (13.9 mm) in heifers with three-wave cycles[15]. Similarly, Sartori et al. reported the size of the ovulatory follicles (14.8 mm) in Holstein heifers. But the observed follicle size was a little bit larger (17.4 mm) in the case of lactating dairy cows[47].

Most follicular waves occur in cycling cattle. However there are some reports that follicular waves also happen in anovulatory circumstances such as before puberty[11] and after puberty[49]. In addition to that, calves with two months of age display follicular waves[11]. Beef and dairy cattle have follicular waves before onset of cyclicity[39,49]. Moreover, there are some reports showing the emergence of follicular waves occurred during pregnancy. But the size of dominant follicles declines from 15.7 mm in diameter in the first wave to 13.1 mm in the second wave during pregnancy[15]. Near the end of pregnancy it reduces to 8.5 mm[17]. In a recent study using Holstein cows with twin and single conceptions by ultrasonography, it was displayed that the number of CL was related in negative way with both embryonic loss and abortive conception during twin calving pregnancy of cows[53]. In general, it can be concluded that the emergence of the follicular wave either in ovulatory or anovulatory circumstances occurs and regulates the physiological functions of the ovary in cattle. Furthermore, some other factors, such as dietary intake, age, parity, and lactation status of animals might influence the number of waves during an estrous cycle.

Regulation of Ovarian Follicular Development

Changes in ovary morphology are observed during normal estrous cycles in dairy cattle. The functions of the ovary are controlled by the cyclic pituitary gonadotropic hormones, which are stimulated by gonadotropin releasing hormone (GnRH) from the hypothalamus. Specifically, the patterns of follicular growth are closely associated with a surge in circulating gonadotrophin hormones[1]. Especially, a high level of circulating follicle-stimulating hormone (FSH) is needed at both first and second onset of the follicular waves. Moreover, selection of the dominant follicle depends upon a drop in FSH level. Wiltbank et al. suggested that FSH has two surges, which are difficult to distinguish from each other during the time close to onset of estrous[60]. But it is clear that GnRH and LH surges, which play critical roles in ovulation, are encouraged by the first FSH surge. The selected dominant follicle is activated to grow by increasing LH concentration and eventually ovulates. A second surge in FSH level is the trigger for the arising of the first wave. After selection of the dominant follicle, subordinate follicles regress due to a low level of FSH.

A reduced expression of the growth hormone/insuline-like growth factor-1 (IGF-1) binding protein is also necessary to continue the development of the dominant follicle at a low level of FSH concentration[36]. IGF-1 also plays an important role by regulating the process of ovarian follicular growth. Studies showed that IGF-1 level in follicular fluid were enhanced as the size of the follicle was larger in diameter. In addition, progesterone concentration is positively correlated with IGF-1 level in follicular fluid across follicles[55]. Echternkamp et al. studied whether selection for twin calving was causing a change in concentrations of IGF-1, progesterone, and estradiol within peripheral blood and IGF-1 and progesterone levels in the ovarian follicular fluid. They observed that twin bearing cows had a larger number of follicles (≥ 4 mm) and 47 % higher IGF-1 concentration in peripheral blood than those of unselected (control) cows. Moreover, cows selected for high twinning rate had a higher concentration of IGF-1 in the two largest follicles than those of control cows (327 ± 28 vs. 243 ± 29 ng/ml; respectively. They indicated that increasing IGF-1 level in both peripheral blood and follicular fluid is closely related to a naturally occurring incidence of twinning in cattle[6]. Development of more than single ovarian follicles at the same time in twin-bearing cows is possibly due to the prevented regression of the dominant follicle caused by increased level of IGF-1. Therefore, IGF-1 may play a critical role in not only the regulation of the stages of the folliculogenesis but also in the genetic basis of multiple ovulations in cattle.

Incidence of Double Ovulations

In rare situations, synchronous emergence of two follicles happens and both of them are selected to take the place of dominant follicles among the several follicles in the follicular wave. Ultimately two oocytes are released from co-dominant follicles at the end of ovulation due to either natural stimulation or artificial inducements. Therefore, twins, or triplets in rare situations, will be a reality if all subsequent events occur in a normal way for both oocytes from fertilization to parturition. Ovulation of two follicles occur either from the same ovary at the same time or each follicle from a separate ovary[59]. Simultaneous production of two oocytes from different follicles were observed due to the evidence of two CL on ovaries of cattle selected for twinning at the USDA - Meat Animal Research Center (MARC) in Nebraska[6]. Also, research about follicular development during the estrous cycle in twin-calving cows indicated that double and triple ovulations occur simultaneously from different ovulatory follicles of the same follicular wave rather than ovulation of single mature follicles from two consecutive waves[7]. In addition, growth hormone and nutritional treatments greatly influence a multiovulation response of an individual[58]. Silva del Rio et al. recently indicated that the cysts in ovary and lack of CL possibly increased the incidence of double ovulations during pregnancy. Also the ovulations of two follicles simultaneously caused to increase days of milk among the pregnant animals[53].

Some of the Factors Affecting Twin Calving Frequency in Cattle

The Effect of Breed Differences

Multiple births; mostly twinning are natural characteristics in some species. This may be a highly desirable trait, which indicates an increased reproductive capacity of an animal. However, in a uniparaous species, like a cow, multiple births occur rarely. It was well documented that there was a considerable variability in a frequency not just only among dairy or beef breeds[24], but also for families within herds, and offspring of sires within breeds[30]. However Hewitt stated that twin births in cattle breeding are most frequent compared with quadruplets or triplet births[20]. Johansson et al. found an average twinning frequencies of 1.9% in dairy, and 0.45% in Finnish and Swedish beef breeds, which could be explained partly by different sources of data[23]. However, some of the variation in the incidence of twinning was observed due to the effect of real breed differences as well as some environmental factors. Many other studies reported similar findings in terms of estimating twinning incidence range on account of breed differences[10,20,34]. Another long-term research study was begun in the early 1930's to select Angus cattle for multiple birth. Over 25 years of data collection, the frequency of multiple calves was 1.71% in this herd[35]. Researchers were not able to compare the estimated frequency since there was no control herd established in the beginning. Relatively few reports on twinning rates in beef cattle were published in the literature in early 20th century. In 1920, Jones and Rouse calculated twinning frequency of 0.41 and 0.45% in American Hereford and Aberdeen-Angus breeds, respectively[19]. According to Hendy and Bowman, these estimates seem to be such a low prediction. One reason could be that females born twin to males would rarely be registered due to freemartinism. High mortality rate among twins could be another reason. Lush worked with Holstein cows at the Kansas Experiment Station and reported that the frequency of twinning in the Holstein breed (8.84%) was five times higher than the other dairy cows in the station[30]. It was obvious that some of the families gave multiple births which means that a certain sire contributed highly for the production of twins. Hewitt conducted a study with the Red Poll breed; 26 out of 1260 births were recorded as twins, which was 2.5%. Six out of 200 Friesian births were also recorded as twin births (3%)[20]. In 1957, Meadow and Lush summarized twin births among dairy cattle in the USA. They reported the lowest twinning rate of 1.31% in Jersey, and the highest twinning frequency of 8.85% in Brown Swiss[34]. Their calculation for Brown Swiss was less reliable for the general twinning tendency since the observed number of births was very low (305) relative to the others. Their estimation for twinning frequency was 3.08% of the total of 10,885 births. Overall, their findings supported the indications of differences between dairy cattle breeds. Over 7300 calvings in Holstein-Friesian herds covering a 30-year period acquired by Erb and Morrison[9], a multiple birth rate of 4. 58% was observed, which was a little bit higher than Meadow and Lush's calculation in two years ago. Two of 338 multiple birth were triplets. Erb et al. also reported a similar rate (4.2%) in a large Holstein-Friesian herd[10]. Additionally, contributions of sire and dam, in addition to breed factors, to multiple births (especially, to the twinning tendency) were noticeable.

Twinning rates for a variety of cattle breeds have been estimated and categorized by breed and country differences. In a review of twinning incidence in different cattle breeds, Hendy and Bowman reported estimates of the twinning incidence for American Holstein-Friesian ranged from 1.92 to 5.02%. Overall twinning rates of beef and dairy breeds, however, were found between 0.34 and 4.50%[19]. Likewise, Gilmore's summary reported a 1.04% average twinning rate in dairy breeds, with the lowest mean rate of 1.18% in Jersey[14]. Even though breed differences play important roles on twinning, it could be confounded by location and country differences. Rutledge summarized extensive field data from American dairy and beef breeds, most of European dairy breeds, and even a few *Bos Indicus* and buffalos[46]. His estimation for twinning rate was 0.4 to 1.1 % for beef breeds such as Angus, Hereford, and Shorthorn and 1.3 to 8.9% for dairy breeds; such as Holstein, Jersey, and Brown Swiss. Unlike the lower twinning frequency reported for beef breeds, in general by Rutledge[46], twinning rates for Charolais were estimated at least 2% higher than traditional British beef breeds by Johansson et al.[23]. In general, twinning rate was found to be mostly higher in breeds of dairy cattle than beef cattle[19]. Also, small sized cattle breeds tended to have twins at lower frequency[46].

Twinning rate differs widely between herds within breed. Nielen et al. studied twinning on Dutch dairy farms. They estimated 3.2% for overall incidence of multiple births from over 11,500 calvings record with a range of 0.0 through 7.11% among herds. However, they did not find a statistically significant difference between Dutch Friesians and Holstein Friesian crossbreds[40]. Similarly, data from 260 North American dairy farms displayed a mean twinning rate of 2.44%; twinning ranged among herds from 0.0 to 9.6%[26]. Morris and Day reported that a Milking Shorthorn herd was found to have high rates of double ovulation (32%) and twinning (6%) among eight breed groups, including Friesian, Angus, Simmental, Charolais, and their crosses. They also reported similar findings about ovulation rates obtained from Friesian herds with high twinning rate. From data on a sample of the Swedish Friesian breed, the mean twinning rate was estimated as 2.57%[38].

Several studies displayed that Holstein-Friesian had the highest twinning frequency in dairy cattle. Twinning rate for purebred Holstein was 4.75% in North America from about 24,000 calving data examined[3]. In contrast, Jersey was the lowest breed in terms of twinning rate (1.83%). Similarly, from about 8,500 calving records on Israeli Holstein herds, the twinning rate was 5.84%, which was slightly over the national average of 4.7% from 1984 to 1985[33]. This increment was most probably due to selection for higher yield and intensive feeding management. In another study including 5300 cows' records from 14 Holstein farms in California, twinning rate was 6.86%[5]. On the other hand, among breeds, such as Ayrshire, Friesian, and Finncattle, Finncattle had more twinning incidence (4.33%) than the others. But the number of calving records evaluated for this breed was lower than the other breeds[31]. Ayrshires had over 1.35 million calving records with 2.38% twin births. Likewise, in a report using over 1.3 million records in North American Holsteins from 1994 to 1998, Johanson et al. calculated a twinning rate of 5.02%[22]. There has been an obvious trend of more twin births in several cattle breeds, especially in Holstein. Also twinning rate was reported to be 10 to 15% in some Holstein herds, depending on the management and feeding systems[13]. A recent estimation about a type of twin calving displayed that a monozygotic twinning was very rare among Holstein pregnant cows, thus most of twin pregnancies observed in Holstein cows were in dizygotic nature[51]. On the other hand, the evaluation of twinning rates in other dairy breeds is not feasible since the recorded twinning incidences for these breeds are not enough to make such a good assessment. Therefore, a large number of calving records are definitely necessary to evaluate the twinning tendency accurately.

Environmental Effects on Twin Calving Frequency in Cattle

Many studies showed that part of the variation in twinning rate must also be due to some environmental factors including parity, age of the dam, and also a season of the year[19,46]. Age and parity of dam affect twin calving significantly and they are highly correlated environmental causes[19].

Effects of Parity and Age of Dam

In general, an increase in twinning rate was observed between first parity and second parity in heifers. Twin pregnancies continue to rise during subsequent parities but to a lesser degree. Johansson et al. reported a rise in the frequency of multiple births up to 5 years of age, which was followed by a slower increase in the frequency up to 10 or 11 years of age and then remained constant in subsequent calvings in Scandinavian breeds of cattle[23]. Likewise, Pfau et al. studied Holstein-Friesians in an experimental herd. Results were tabulated where age of dam was expressed as a number of parturitions. Twinning rate was low at the beginning (0.74%), after that it dramatically increased (5.03%) with age from second parity, then it leveled at fifth through seventh parities (7.79, 9.80, and 7.32%, respectively). After seventh parturition, it started again to decline (4.35%)[41]. Even if Hewitt displayed no consistency in the rate of twinning with increasing parity, it was more probably due to the differences in the number of calving cows at various ages[20]. Calving data from cows sired by Norwegian Red sires showed a twinning rate of 6.7% in parity 1, of 9.2% in parity 2, and of 8.6% in later parities[56]. Erb and Morrison worked with Holstein data covering a 30 year period and found a significant parity effect on twinning rate of 1.3% for heifers and 4.4% for second calving cows[9]. They also observed that twinning rate was consistently increased up to 7.1% from second to tenth parities even if it was not found statistically significant. After 10 years of age, cows had a reduction in twinning frequency. Bar-Anan and Bowman worked with Israeli-Friesian herds. They demonstrated twinning incidence of 0.7 and 5.4% in heifers and cows, respectively in large herds, however, observed twinning rates were 0.7 and 3.5% for those kinds of animals, respectively in small herds[2]. The high twinning rate might be due to the high level of feeding, milk yield, and intensive management system.

Johansson and colleagues summarized calving records from different cattle breeds and published important breed and parity, and age of dam effects on the frequency of both monozygous and fraternal twin rates.Twinning tendency was enhanced 4-5 times from first to subsequent calving. Also, the increase in dizygotic twin frequency was much higher than the increase in monozygotic twinning rate from the fifth and later parities[23]. It seems that monozygotic twin rate does not depend on parity. On the other hand, the parity effect on twinning rate is most likely due to the increased fraternal twin frequency and enhanced double ovulation rates. Therefore, even if some studies have shown that increased uterine capacity of the dam might be the probable reason of increased the incidence of twin calving[44], other studies have indicated that increased rate of ovulation is one of the critical factors related to the parity effect on twinning frequency[28]. Fricke and Wiltbank also studied cows in lactation and showed enhanced multiple ovulation tendencies along with parity and the age of dam[12].

Cady and Van Vleck worked with U.S. Holstein cattle and observed a significant increase in twinning rate as parity and cow's age increased[3]. Frequencies were 1.05% for first parity to 6.18% for third and later parities, which was in agreement with Markusfeld's findings in the Israeli-Holstein population[33]. Cady and Van Vleck, on the other hand, did not observe a significant contribution of some factors, such as a month of birth and size of dam measured in different parities[3]. Nielen et al. reported that cows, which had twin births in previous parities, were more likely to give multiple births again in subsequent calving seasons[40]. Moreover, Maijala and Osva conducted a study with Finnish Ayrshire and Friesian cattle and found the frequency of twinning from first to second parities and from second to third parities increased about 2% and 1%, respectively[31]. Second and third parity twinning rates of Israeli-Holstein cows were analyzed by linear and threshold models; twinning rates were 4.8 and 6.9% for the second and third parities, respectively[45]. In this population, first parity records were deleted because of the low incidence of twinning. Ryan and Boland studied Holstein-Friesian cows in dry climate conditions and reported increasing twinning rate from 1% at first calving to 8% for all the subsequent calvings. They observed a similar twinning rate (7-7.8%) at second through fourth calving seasons; the greatest frequency (9.1%) was obtained in ninth parity[44]. However, twinning rates in the first and second parities were found very low in New Zealand twinning herd by Morris[37]. The reason might be that young cows have difficulty maintaining a twin pregnancy and thus usually abort the fetuses. Twinning rates increased rapidly up to 5 years of age and it continued to rise slowly up to 10 or 11 years of age.

The reason for parity effects on incidence of multiple births are still not completely clarified, but what could be possibly happening is that older dams have more chance to have more incidence of double ovulation physiologically and have more ability to support developmental of twin calves throughout the pregnancy. Indeed, Rutledge stated that older cows have a tendency to calve more twins than younger counterparts[46]. Moreover, he argued that the incidence of the multiple births is probably underestimated due to the higher culling rate at certain ages of cows.

Data was collected from the Maine-Anjou breed between 1972 and 1990 in French beef herds[32]. A consistent increase in twin calving rate across parities was detected. Moreover, twinning frequency of cows was almost twice the frequency in heifers. The difference between parities obviously reflects the importance of this factor on twinning. Kinsel and colleagues used over 50,000 lactation records over a 10-year period from 260 dairy farms in North America. They stated that the rate of twinning increased as the parity of the cow increased from 1.0% for first lactation to more than 4.1% for cows in their fifth or higher lactations[26]. However, they did not find any significant association between twinning and the season of conception, which is consistent with the findings of Eddy et al.[8] but in contrast to the report by Nielen et al.[40]. Similarly, Syrstad worked with Norwegian dairy cattle and reported twinning rates of 0.46% for first parity and 3.57% for fifth parity[57]. Karlsen and colleagues also demonstrated a positive upward trend in overall twinning frequency from the first parity (0.6%) through fourth parity (4.0%) in the Norwegian cattle population[25]. Likewise, Johanson et al. reported a tendency of increasing twinning rate from the first to second parity; 1.63 and 5.22%, respectively[22]. In recent studies with North American Holstein[52] and Iranian Holstein[21] cows were also indicated that calving season and parity of cow were important factors which highly related with twin calving incidence during pregnancy.

Other factors, such as milk yield, could be confounded with the effect of cow's age and parity on twinning rate and could help to understand variability of twin birth ratio caused by parity and the age of dam.

The Effect of Season of the Year

Differences in twinning rate between calving seasons have also been reported. Several studies have shown the effect of season on twinning rate; however, some others have failed to prove such an effect.

Peak twinning rate of 0.5% was observed for cows conceiving in the fall season and lowest frequency (0.3%) in the spring season[24]. Johansson et al. also reported a seasonal influence on the frequency of twinning. A high peak frequency was observed in June and a lower peak in December and January in the Scandinavian breeds[23]. Likewise, Ryan and Boland reported a highly significant season effect on percentage of twin births within all calving seasons (second to fifth parities) except for those in first parity[44]. The reason could be a reduced photoperiod and an improved feeding in the fall season. A relatively small increase in twinning frequency during the summer (especially, June and July) was also reported by Cady and Van Vleck[3]. This could also be due to a better feeding in autumn. Moreover, Johansson and colleagues reported the relation of twin frequencies with conception period in Danish and Swedish dairy cows. They reported a twinning rate between 0.5-1.36% in September – November periods, and 0.39-0.70% in December – May. In addition, they observed high twin frequencies of 2.85% and 3.19% in May and October – December, respectively at the fourth parity in German breeds of cows[23]. Therefore, they reported a maximum rate of twinning in spring as well as autumn conception periods. According to Ryan and Boland, higher mortality rate in hot months, compared with cool months, could be the major reason of observed high twinning incidence[44].

Hendy and Bowman reviewed several studies in terms of environmental effects on twinning frequency of cattle. They reported seasonal variation in twinning from different studies even if some of them have not been statistically significant[19]. For example, in studies conducted in Australia[20], there was no significant variation between monthly twinning rates due to season of the year. The reason could be the prevailing mild climate in that region. Ryan and Boland reported twinning rate was observed at the peak level of 9.3% for second parity and averaged 13.1% for later parities in May through June months. On the other hand, twinning rate was detected at the lowest level of 3.9% for parity 2 and averaged 4.1% in later parities between January and February[44]. Rutledge reviewed the effect of season on twinning rate. He concluded that twinning rate was high in fall (2.2%) and at spring (1.9%) but it was low in winter and summer (1.5%)[46]. However, some researchers did not evaluate the seasonal effect on twinning tendency due to lack of collected records on it. Other factors, such as feeding management, nutrition level, light period and temperature are most probably important sources that are triggers for the effect of season on twinning incidence.

From the Dutch cattle population, Nielen and colleagues found that season had a significant role on twinning percentage. The odds ratio of multiple births in April through September was 1.3, as compared with a period from October through March[40]. In the MARC twinning population Gregory et al. reported greater twinning frequency (1.13) in the fall season, compared with spring (1.06)[18]. According to Schillo and colleagues, photoperiod could have an effect on twin births[50]. A study with Norwegian cattle breeds also demonstrated a seasonal effect related with twinning. They showed a peak in March for cows in second parity, which was more probably due to the turn out on pasture in June in Norway[25].

Twinning rate was also slightly influenced by seasonal effect with a trend toward more multiple births during the spring[3] or autumn months[18] in North American dairy populations. On the other hand, Kinsel et al. studied North American Dairy farms and were not able to find a significant relationship between season and twinning rate[26]. Eddy et al. also could not report statistically important seasonal effects[8]. However, Johanson et al., studying North American Holsteins, reported a seasonal effect that was higher on twinning rate (5.88%) in April through June and October to December (4.23%)[22].

Even though an increased chance of twin births in summer season could be related with decreased photoperiod and temperature and increased intensive feeding and management in fall seasons, further research would be needed to confirm the effects of the factors causing seasonal changes in twinning frequencies.

Conclusion

It is obvious that a complete understanding of the complex process of follicular growth during estrus cycle and the development of oocytes will certainly improve the knowledge to maximize and control the efficiency of reproduction in livestock species, especially the existence of dizygotic twinning since the fertilization of more than one oocyte after ovulation will be the main reason of multiple births. On the other hands, several studies indicated that many genetic and environmental factors, specifically age and parity of dams, season of calving period and also breed differences mostly affects twin calving rates importantly in dairy and beef cow production systems.

References

1. Adams, G. P., Matteri, R. L., Kastelic, J. P., Ko, J. C. H., and Ginther, O. J., 1992. Association between surges of FSH and emergence of follicular waves in heifers. *J. Reprod. Fertility,* 94, 177-188.
2. Bar-Anan, R. and Bowman, J. C., 1974. Twinning in Israeli Friesian dairy herds. *Anim. Prod.*, 18, 109-115.
3. Cady, R. A. and Van Vleck, L. D., 1978. Factors affecting twinning and effects of twinning in Holstein Dairy cattle. *J. Anim. Sci.*, 46, 950-956.
4. Campbell, B. K., Scaramuzzi, R. J., and Webb, R., 1995. Control of antral follicular development and selection in sheep and cattle. *J. Reprod. Fertility.*, 49, 335-350.
5. Day, J. D., Weaver, L. D., and Franti, C. E., 1995. Twin pregnancy diagnosis in Holstein cows: discriminatory powers and accuracy of diagnosis by transrectal palpation and outcome of twin pregnancies. *Can. Vet. J.*, 36, 93-97.
6. Echternkamp, S. E., Spicer, L. J., Gregory, K. E., Canning, S. F., and Hammond, J. M., 1990a. Concentrations of insulin-like growth factor-I in blood and ovarian follicular fluid of cattle selected for twins. *Biology of Reprod.*, 43, 8-14.
7. Echternkamp, S. E., 2000. Endocrinology of increased ovarian folliculogenesis in cattle selected for twin births. *Am. Society of Anim. Sci.*,1-20.
8. Eddy, R. G., Davies, O., and David, C., 1991. An economic assessment of twin births in British dairy herds. *Vet. Rec.*,129, 526-529.
9. Erb, R. E. and Morrison, R. A., 1959. Effects of Twinning on reproductive efficiency in a Holstein-Friesian herd. *J. Dairy Sci.*, 42, 512-519.
10. Erb, R. E., Anderson, W. R., Hinze, P. M., and Gildow, E. M., 1960. Inheritance of twinning in aherd of Holstein-Frieasian cattle. *J. Dairy Sci.*, 4, 393.
11. Evans, A. C. O., Adams, G. P., and Rawlings, N. C., 1994. Follicular and hormonal development in prepubertal heifers from 2 to 36 weeks of age. *J. Reprod. Fertility.*, 102, 463-470.
12. Fricke, P. M. and Wiltbank, M. C., 1999. Effect of milk production on the incidence of double ovulation in dairy cows. *Theriogenology*, 52, 1133-1143.
13. Fricke, P. M., 2001. Review: Twinning in Dairy Cattle. *The Professional Animal Scientis,*. 17, 61-67.
14. Gilmore, L. O., 1952. Dairy Cattle Breeding. J. B. Lippincott Company, Philadelphia, Pennsylvani-USA.
15. Ginther, O. J., Knopf, L., and Kastelic, J. P., 1989a. Temporal associations among ovarian events during bovine oestrous cycles with two and three follicular waves. *J. Reprod. Fertility*, 87, 223-230.

16. Ginther, O. J., Knopf, L., and Kastelic, J. P., 1989b. Ovarian follicular dynamics in heifers during early pregnancy. *Biology of Reprod.*, 41, 247-254.

17. Ginther, O. J., Wiltbank, M. C., Fricke, P. M., Gibbons, J. R., and Kot, K., 1996. Selection of the dominant follicle in cattle. *Biology of Reprod.*, 55, 1187-1194.

18. Gregory, K. E., Echternkamp, S. E., Dickerson, G. E., Cundiff, L. V., Koch, R. M., and Van Vleck, L. D., 1990a. Twinning in cattle: I. Foundation animals and genetic and environmental effects on twinning rate. *J. Anim. Sci.*, 68, 1867-1876.

19. Hendy, C. R. C. and Bowman, J. C., 1970. Twinning in cattle. *Animal Breeding Abstracts*, 38, 22-37.

20. Hewitt, A. C. T., 1934. Twinning in cattle. *J. of Dairy Research*, 5, 101-107.

21. Hossein-Zadeh, N.G., Nejati-Javaremi A., Miraei-Ashtiani S.R., and Kohram H., 2008. An observational analysis of twin birds, calf stillbirds, Calf sex ratio, and abortion in Iranian Holsteins. *J. Dairy Sci,* 91, 4198-4205.

22. Johanson, J. M., Berger, P. J., Kirkpatrick, B. W. and Dentine, M. R., 2001. Twinning rates for North American Holstein sires. *J. Dairy Sci.*, 84, 2081-2088.

23. Johansson, I., Lindhé, B., and Pirchner, F., 1974. Causes of variation in the frequency of monozygous and dizygous twinning in various breeds of cattle. *Hereditas*, 78, 201-234.

24. Jones, S. V. H. and Rouse, J. E., 1920. The relation of dam to observed fecundity in domesticated animals. I. Multiple births in cattle and sheep. *J. Dairy Sci.*, 3, 260.

25. Karlsen, A., Ruane, J., Klemetsdal, G., and Heringstad, B., 2000. Twinning rate in Norwegian cattle: frequency, (co)variance components, and genetic trends. *J. Anim. Sci.*, 78, 15-20.

26. Kinsel, M. L., Marsh, W. E., Ruegg, P. L., and Etherington W. G., 1998. Risk factors for twinning in dairy cows. *J. Dairy Sci.*, 81, 989-993.

27. Knopf, L., Kastelic, J. P., Schallenberger, E., and Ginther, O. J., 1989. Ovarian follicular dynamics in heifers: test of two-wave hypotheses by ultrasonically monitoring individual follicles. *Domestic Animal Endocrinology*, 6, 111-119.

28. Labhsetwar, A. P., Tyler, W. J., and Casida, L. E, 1963. Analysis of variation in some factors affecting multiple ovulations in Holstein cattle. *J. Dairy Sci.*, 46, 840.

29. Lucy, M.C., Savio, J. D., Badinga, L., De La Sota, R. L., and Thatcher, W.W., 1992. Factors that affect follicular ovarian dynamics in cattle. *J. Anim. Sci.*, 70, 3615-3626.

30. Lush, R. H., 1925. Inheritance of twinning in a herd of Holstein cattle. *The J. of Heredity*, 16, 273-279.

31. Maijala, K. and Osva, A., 1990. Genetic correlations of twinning frequency with other economic traits in dairy cattle. *J. Anim. Breed. Genet.*, 107, 7-15.

32. Manfredi, E., Foulley, J. L., San Cristobal, M., and Gillard, P., 1991. Genetic Parameters for twinning in the Maine-Anjou Breed. Genet. Sel. Evol**.**, 23, 421-430.

33. Markusfeld, O., 1987. Periparturient traits in seven high dairy herds. Incidence rates, association with parity, and interrelationships among traits. *J. Dairy Sci.* 70, 158-166.

34. Meadows, C. E. and Lush, J. L., 1957. Twinning in dairy cattle and its relation to production. *J. Dairy Sci.*, 40, 1430-1436.

35. Mechling, E. A. and Carter, R. C., 1964. Selection for twinning in a Grade Aberdeen-Angus Herd. *The J. of Heredity*, 55, 73-75.

36. Mihm, M., Good, T. E., Ireland, J. L., Ireland, J. J., Knight, P. G., and Roche, J. F., 1997. Decline in serum follicle-stimulating hormone concentrations alters key intrafollicular growth factors involved in selection of the dominant follicle in heifers. *Biology Reprod.*, 57, 1328-1337.

37. Morris, C. A., 1984. A review of the genetics and reproductive physiology of dizygotic twinning in cattle. *Anim. Breeding Abstracts*, 52, 803-819.

38. Morris, C. A. and Day, A. M., 1986. Ovulation results from cattle herds with high twinning frequency. 96-100 in Proceedings 3rd World Congress on Genetics Applied to Livestock Production. Lincoln, Nebraska-USA.

39. Murphy, M. G., Boland, M. P., and Roche, J. F., 1990. Pattern of follicular growth and resumption of ovarian activity in post-partum beef sucker cows. *J. Reprod. Fertility*, 90, 523-533.

40. Nielen, M., Schukken, Y. H., Scholl, D. T., Wilbrink, H. J., and Brand, A., 1989. Twinning in dairy cattle: a study of risk factors and effects. *Theriogenology*, 32, 845-862.

41. Pfau, K., Bartlett, O. J. W., and Shuart, C. E., 1948. A study of multiple births in a Holstein-Friesian herd. *J. Dairy Sci.*, 31, 241-254.

42. Pierson, R. A. and Ginther, O. J., 1984. Ultrasonography of the bovine ovary. *Theriogenology*, 21, 495-504.

43. Rajakoski, E., 1960. The ovarian follicular system in sexually mature heifers with special reference to seasonal, cyclical, and left-right variation. *Acta. Endrocrinol.*, 34 (suppl.52), 7-68.

44. Ryan, D. P. and Boland, M. P., 1991. Frequency of twin births amond Holstein-Friesian cows in a warm dry climate. *Theriogenology*, 36, 1-10.

45. Ron, M., Ezra, E., and Weller, J. I., 1990. Genetic analysis of twinning rate in Israeli Holstein Cattle. Genet. Sel. Evol**.,** 22, 349-359.
46. Rutledge, J. J., 1975. Twinning in cattle. *J. Anim. Sci.*, 40, 803-815.
47. Sartori, R., Haughian, J., Rosa, G. J. M., Shaver, R. D., and Wiltbank, M. C., 2000. Differences between lactating cows and nulliparous heifers in follicular dynamics, luteal growth, and serum steroid concentrations. *J. Dairy Sci.*, 83(Suppl 1), 212.
48. Savio, J. D., Keenan, L., Boland, M. P., and Roche, J. F., 1988. Pattern of growth of dominant follicles during the oestrous cycle in heifers. *J. Reprod. Fertility*, 83, 663-671.
49. Savio, J. D., Boland, M. P., and Roche, J. F., 1990. Development of dominant follicles and length of ovarian cycles in post-partum dairy cows. *J. Reprod. Fertility*, 88, 581-591.
50. Schillo, K. K., Hall, J. B., Hileman, S. M., 1992. Effect of nutrition and season on the set of puberty in the beef heifers. *J. Anim. Sci.*, 70, 3994-4005.
51. Silva del Rio, N., Kirkpatrick B.W., Fricke P.M., 2006. Observed frequency of monozygotic twinning in Holstein dairy cattle. *Theriogenology,* 66, 1292–1299.
52. Silva del Rio, N., Stewart S., Rapnicki P., Chang Y. M., and Fricke P.M., 2007. An Observational Analysis of Twin Births, Calf Sex Ratio, and Calf Mortality in Holstein Dairy Cattle. *J. Dairy Sci.,* 90, 1255–1264.
53. Silva del Rio, N., Colloton J.D., Fricke P.M., 2009. Factors affecting pregnancy loss for single and twin pregnancies in a high-producing dairy herd. *Theriogenology,* 71, 1462–1471.
54. Sirois, J. and Fortune, J. E., 1988. Ovarian follicular dynamics during the estrous cycle in heifers monitored by real-time ultrasonography. *Biology. Reprod.*, 39, 308-317.
55. Spicer, L.J., Echternkamp, S. E., Canning, S. F., and Hammond, J. M., 1988. Relationship between concentrations of immunoreactive insulin-like growth factor-I in follicular fluid and various biochemical markers of differentiation in bovine antral follicules. *Biology. Reprod.*, 39, 573-80.
56. Syrstad, O., 1974. Genetic aspects of twinning in dairy cattle. *Acta. Agricult Scandinavica*, 24, Issue 4, 319 – 322.
57. Syrstad, O., 1984. Inheritance of multiple births in cattle. *Livestock Production Science*, 11, 373-380.
58. Webb, R. and Armstrong, D. G., 1998. Control of ovarian function; effect of local interactions and environmental influences on follicular turnover in cattle: a review. *Livestock Production Science*, 53, 95-112.
59. Wiltbank, M.C., Fricke, P. M., Sangsritavong, S., Sartori, R., and Ginther, O. J., 2000. Mechanisms that prevent and produce double ovulations in dairy cattle. *J. Dairy Sci.*, 83, 2998-3007.
60. Wiltbank, M.C., Gumen, A., and Sartori, R, 2001. Physiological classification of anovulatory conditions in cattle. *Theriogenology*, 57, 21-52.