Pregnancy in Beef Cattle: Ovarian and Uterine Contributions

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Points to Remember:

Gonadotropin releasing hormone (GnRH)-induced ovulation of a physiologically immature dominant follicle decreases pregnancy rate and decreases late embryonic/fetal survival.

Fertilization rate in donor cows increased as estradiol at insemination increased, ovulatory follicle size increased, and days postpartum increased.

Pregnancy at day 27 in recipient cows increased as estradiol at insemination increased, progesterone at embryo transfer increased, and as ovulatory follicle size decreased. Concentration of estradiol at insemination was directly associated with pregnancy rate and was the most consistent variable affecting fertility. Increased estradiol at the time of insemination in cattle is important for fertilization success and the establishment of pregnancy.

Maintenance of pregnancy in recipient cows increased as embryo quality increased.

Understanding the factors affecting the establishment and maintenance of pregnancy is complicated and requires simultaneous consideration of numerous variables. Much of the biology underlying establishment and maintenance of pregnancy remains to be determined.

Introduction:

Synchronization of dominant follicle development and control of ovulation are commonly used assisted reproductive technologies in cattle. The final maturation of the dominant follicle is intimately tied to the final maturation of the oocyte, preovulatory secretion of estradiol, postovulatory secretion of progesterone, and endocrine control of the oviductal and uterine environment for gamete and embryo development. The physiological maturity of a dominant/ovulatory follicle can affect the establishment and maintenance of pregnancy. Induction of ovulation in a dominant follicle that has not acquired physiological maturity can reduce pregnancy rates and increase late embryonic/fetal mortality in cattle, which is likely mediated through inadequate oocyte competence and a compromised maternal environment. Oocyte competence increases with follicular maturity and preovulatory secretion of estradiol is a reflection of follicular maturity and affects the oocyte, follicular cells, oviduct, and uterus. The corpus luteum is a continuation of follicular maturation and rate of progesterone secretion following ovulation is linked to fertility. Advancements in our understanding of how the follicular microenvironment affects pregnancy establishment and maintenance will likely increase pregnancy rates to fixed-time artificial insemination (FTAI).

Protocols that synchronize ovulation in cattle for purposes of insemination at a fixed-time commonly include an injection of GnRH (GnRH-1) to induce ovulation and corpus luteum formation as well as initiate a new follicular wave. After five to seven days cows are injected with prostaglandin $F_{2\alpha}$ (PGF) to induce luteolysis and 60 to 72 hr (day 0) GnRH (GnRH-2) is administered to induce ovulation (Figure 1). Insemination occurs at the time of the second GnRH injection. GnRH-induced ovulation of follicles ≤ 11 mm resulted in decreased pregnancy rates and increased late embryonic mortality (Perry et.al., 2005). This decrease in fertility was associated with lower circulating concentrations of estradiol on the day of insemination, a decreased rate of increase in progesterone following insemination, and, ultimately, decreased circulating concentrations of progesterone. In contrast, ovulatory follicle size had no apparent effect on fertility when ovulation occurred spontaneously. Follicles undergoing spontaneous ovulation do so at a wide range of sizes when they are physiologically mature. Therefore, in cows with a small dominant follicle administration of GnRH may induce ovulation before a dominant follicle has attained physiological maturity. GnRH-induced ovulation of follicles that are physiologically immature has a negative impact on pregnancy rates and late embryonic/fetal survival. These observations in cattle have implications for estrus synchronization protocols in which GnRH-induced ovulation occurs at insemination.

To determine why pregnancy rates were decreased following GnRH-induced ovulation of small dominant follicles, a reciprocal embryo transfer (RET) experiment was conducted to understand how ovulatory follicle size effects the establishment and maintenance of pregnancy in postpartum beef cows(Atkins, 2009; Atkins et. al., 2010a). The design of the RET experiment and the results are described below.

Experimental Design:

This experiment occurred over three breeding seasons with suckled postpartum beef cows. The timeline for data collection in each year is illustrated in Figure 2. Suckled beef cows (n = 2,550) were synchronized with the CO-Synch protocol (GnRH [GnRH-1] on day -9 followed by PGF on day -2 and GnRH [GnRH-2] on day 0 with fixed-timed artificial insemination [AI]), but only cows that did not exhibit estrus before or after GnRH-2 (n = 1,164) were used. Body weights and BCS (scale of 1 to 9 where 1 = emaciated and 9 = obese; 67) were obtained on day -9 (GnRH-1). Donor cows (n = 810) were inseminated by one of three AI technicians with semen from one sire (three collections). Single embryos (n = 394) or oocytes (n = 45) were recovered from the donor cows by uterine horn lavage 7 days after AI (day 0) and all live embryos (n = 354) were transferred into recipients the same day. Embryos from cows that ovulated a small (< 12.5 mm) or large follicle (≥ 12.5 mm) were transferred into cows that ovulated either a small or large follicle to remove co-linearity of follicle sizes pre- and post- day 7 of pregnancy; small to small (S-S; n = 71), small to large (S-L; n = 111), large to small (L-S; n = 122) and large to large (L-L; n = 50). The small to small group served as a negative control since these transfers should result in the lowest pregnancy rate. Similarly, the large to large group was expected to result in the highest pregnancy rate; therefore, this group served as a positive control. The small to large transfer was designed to test the effect of transferring an embryo derived from ovulation of a small follicle into a uterine environment established by ovulation of a large follicle on pregnancy rate. A pregnancy rate similar to the small to small group might reflect a problem with oocyte competence. The large to small transfer group was designed to test the effect of transferring an embryo derived from ovulation of a large follicle into a uterine environment established by ovulation of a small follicle on pregnancy rate. A pregnancy rate similar to the small to small group might reflect a problem with the maternal environment.

Statistical analyses were guided by path diagrams in which potential cause-effect relationships among the measured variables were hypothesized (Wright 1934). Single trait comparisons for biologically complex mechanisms (e.g. pregnancy) can lead to different conclusions compared to the path analysis approach. For example, an analysis of the effect of ovulatory size on pregnancy rate might reveal a statistically significant effect. However, the effect might not be due to ovulatory follicle size but the amount of estradiol secreted by the follicle before ovulation and (or) the amount of progesterone secreted by the subsequently formed corpus luteum. Path analysis permits multiple biologically important variables (e.g. ovulatory follicle size, estradiol secretion, luteal progesterone secretion, and pregnancy rate) to be accounted for in a single analysis and can yield a deeper level of understanding than when considering any one variable alone. The “r values” reported below are standardized linear regression coefficients which are similar to simple correlation coefficients that measure the strength of the influence of one variable on another. An “r value” approaching 1.0 reflects a strong association; whereas, a number approaching zero reflects a low or no association between two variables. A positive “r value” means a positive association; whereas, a negative “r value” means a negative association between two variables.

Factors Affecting Cyclicity and Ovulatory Response to GnRH-1

The proportion of cycling cows at the start of the experiment was positively affected by days postpartum (r = 0.17), body weight (r = 0.10), and body condition score (r = 0.07). Consequently, cows that were cycling at the start of the experiment tended to be heavier, were in better body condition, and had more days postpartum than anestrous cows. These data emphasize the importance of managing cows to have adequate body condition at calving and to calve early, which will increase the number of days postpartum at the start of the breeding season.

The proportion of cows that ovulated in response to GnRH-1 at the beginning of the CO-Synch protocol was 59% (564/949). Whether or not a cow ovulated following GnRH-1 was directly affected by whether or not she was cycling (r = -0.20), days postpartum (r = 0.13), and body weight (r = 0.07). Cows that were cycling before injection of GnRH-1 were less likely to ovulate at the beginning of the synchronization protocol and this effect was 1.5 to 2.9 times more important than the effect of days postpartum or body weight. Cows that ovulated in response to GnRH-1 had an increased ovulatory follicle growth rate from PGF to GnRH-2 and larger follicle diameter at GnRH-2. These results confirm an early study in which ovulation to GnRH-1 and synchronization of a follicular wave resulted in a larger dominant follicle at GnRH-2 in postpartum beef cows (Atkins et. al., 2010b). Ovulatory response following GnRH-1 likely affected the age of the follicle induced to ovulate following GnRH-2. Lack of an ovulatory response to GnRH-1 may have resulted in the presence of an older follicle at GnRH-2 in some cows since cows that exhibited estrus before GnRH-2 were removed from the study.

From a management standpoint, the proportion of cows that have a dominant follicle capable of responding to GnRH-1 can be increased by presynchronizing the cows. Alternatively, administration of estrogen at CIDR insertion does a better job of follicular wave control than GnRH since estrogen works by decreasing FSH and is not dependent upon the presence of a viable dominant follicle at CIDR insertion (Day et. al., 2010).

Factors Affecting Ovulatory Follicle Size at GnRH-2

Ovulatory follicle size at GnRH-2 was positively affected by follicle growth rate from PGF to GnRH-2 (r = 0.32), body weight (r = 0.14), days postpartum (r = 0.08), and negatively affected by cyclicity status (r = -0.09) and serum progesterone at PGF (r = -0.15). Therefore, cows with larger ovulatory follicle size at GnRH-2 were heavier, had more days postpartum, had lower serum progesterone at PGF, and increased follicle growth rate from PGF to GnRH-2 than cows with a smaller ovulatory follicle. It is interesting that ovulatory follicle size at GnRH-2 was larger in anestrous compared to cycling cows; however, the reason for this is not clear. Since the corpus luteum is a continuation of follicular maturation, it is not surprising that follicle diameter at GnRH-2 was positively correlated with luteal volume and serum concentrations of progesterone at ET (r = 0.46 and 0.31, respectively).

Factors Associated With Fertilization

Fertilization rate (90%) was positively associated with serum estradiol at insemination (r = 0.16), body weight (r = 0.16), days postpartum (r = 0.14), ovulatory follicle size (r = 0.10), and negatively associated with cow age (r = -0.16). Therefore, successful fertilization was enhanced in cows with greater serum concentration of estradiol at insemination, in cows with a longer postpartum period, increased size of the ovulatory follicle, and in cows that were heavier and younger. Induced ovulation of a dominant follicle that has not attained physiological maturity may result in the release of an oocyte that is less capable of being fertilized and forming a viable embryo.

Fertilization rate in beef cattle is normally high (≥ 90%; Sreenan and Diskin, 1983) and the results of the RET study indicate that fertilization rate is decreased when ovulatory follicle size, serum estradiol at insemination, cow body weight, and days postpartum are decreased. Management strategies to increase fertilization rate at FTAI should include the following: 1) Utilize FTAI protocols that increase the physiological maturity (e.g. estradiol secretion) of the ovulatory follicle, 2) Increase the proportion of females that conceive early in the breeding season which will shorten the calving season and thereby increase the number of days postpartum at the subsequent insemination, and 3) Ensure cows have adequate body weight at the time of estrus synchronization.

Factors Affecting Estradiol and Progesterone Around the Time of Insemination

Endocrine status around the time of insemination has an important impact on the establishment of pregnancy and was characterized by measuring serum concentrations of progesterone at PGF, estradiol at insemination, and progesterone at embryo transfer. Elevated serum concentrations of progesterone from the cycle before conception has been associated with increased conception rates (Folman et. al., 1973; Fonesca et. al., 1983; Bello et. al., 2006). While it is not known how elevated circulating concentrations of progesterone from the previous cycle affect conception rate, it is possible that oocyte competence is compromised when circulating progesterone during the cycle before insemination is low.

Progesterone at PGF: The following three factors had important and positive direct effects on serum progesterone at PGF: 1) Ovulation in response to GnRH-1 (r = 0.36), which is presumably due to induction of luteal tissue formation, 2) increased proportion of cycling cows at GnRH-1 (r = 0.30), and 3) body condition score (r = 0.10). Estrous cyclicity and ovulatory response to GnRH1 had large positive effects on serum progesterone concentration at PGF, with a relatively minor additional positive contribution from increased body condition score. Variables having negative effects on serum progesterone concentration at PGF were increased cow age and increased days postpartum.

Estradiol at Insemination: Serum estradiol and ovulatory follicle size at insemination were positively correlated (r = 0.46). We were unable to assign cause and effect to these two variables since an increased number of follicular cells can increase estradiol secretion and increased estradiol can directly affect estradiol secretion by granulosa cells. Serum estradiol at insemination was positively affected by ovulatory response to GnRH-1 (r = 0.07) and progesterone at PGF (r = 0.05) and negatively associated with follicle growth rate (r = -0.07). The effect of ovulatory response to GnRH-1 on serum estradiol at insemination emphasizes the importance of increasing the proportion of cows that respond to GnRH-1.

Progesterone at Embryo Transfer (Day 7): The rate of increase in progesterone following insemination is positively associated with pregnancy rate in cattle (Mann and Laming, 2001; Perry et. al., 2005; Bridges et. al., 2010). In the RET study the following three factors had a direct effect on serum progesterone at embryo transfer (seven days following GnRH-2): 1) serum estradiol at insemination (r = 0.26), serum progesterone at PGF (r = 0.23), and ovulatory follicle size (r = 0.21). Alterations in estradiol and or progesterone around the time of insemination could alter oviductal and uterine environment to impact fertilization success.

Estradiol may affect the oviductal or uterine environment by changing the pH of the uterus (Elrod and Butler, 1993; Perry and Perry, 2008), altering sperm transport and longevity (Allison et. al., 1972; Hawk 1983) to improve fertilization success, oviduct secretions (for example oviductal glycoprotein; Buhi, 2002) and indirectly stimulate progesterone activity through induction of progesterone receptors in the uterus (Stone et. al., 1978; Zelinski et. al., 1982; Ing and Tornesi, 1997).

Mechanisms Associated With Embryo Viability, Stage of Embryo Development and Embryo Quality at Embryo Transfer

Embryonic viability: The percentage of embryos that were dead on day 7 after insemination was only 6% and the major factors that contributed to embryonic death included small ovulatory size (r = 0.17), low serum progesterone at PGF (r = 0.15), increased cow body weight (r = 0.11), and rapid dominant follicle growth rate (r = 0.10). Low progesterone at PGF might indicate failure to ovulate after the GnRH-1 injection and perhaps the presence of a somewhat persistent follicle that ovulated following GnRH-2. Ova from persistent follicles can be fertilized; however, the embryos normally die by the 16 cell stage (Ahmed et. al., 1995).

Stage of embryonic development: The majority of embryos collected in the RET study were at the morula stage followed by early blastocysts, early morulas, 2 to 12 cell embryos, blastocysts and expanded blastocysts (n = 221, 79, 54, 19, 9, and 1). The major factors that directly affected stage of embryonic development included embryonic viability (r = 0.49), ovulatory follicle size (r = -0.13), cow age (r = -0.13), serum progesterone at embryo collection on day 7 (r = 0.11), and ovulatory follicle growth rate (r = 0.10). These data indicate that fertilization of an ovum from a large follicle would result in an embryo that is more viable but at an earlier stage of development than fertilization of an ovum from a small follicle. In addition, fertilization of an ovum from a rapidly growing follicle would be at a more advanced stage of development but would be less viable than fertilization of an ovum from a follicle that grew at a slower rate . The mechanisms underlying the preceding predictions are not clear but may involve differences in the epigenetic modification of the oocyte genome that affects the control of embryonic development and synchrony between an embryo and the maternal environment. It is not surprising that increased serum concentrations of progesterone on day 7 had a positive effect of stage of embryonic development since elevated circulating concentrations of progesterone during early embryonic development have been shown to increase pregnancy rates.

Embryo quality: Of all the factors that were examined only ovulatory follicle size had a significant effect on embryo quality. As ovulatory follicle size increased there was an increase in embryo quality. Although ovulatory follicle size was negatively associated with stage of embryonic development it was positively associated with both embryo quality and viability. Thus, ovulatory follicle size may be an indicator of oocyte competence.

Mechanisms Associated With Pregnancy Establishment

After examining the effect of twelve or more factors on pregnancy rate at day 27 we were only able to account for about 10% of the variation in pregnancy rate. Therefore, much of the biology underlying establishment and maintenance of pregnancy in cattle remains to be determined. The establishment of pregnancy by day 27 was positively affected by serum progesterone at day 7 ($r = 0.23$), serum estradiol at insemination ($r = 0.20$), and cow age ($r = 0.10$). Pregnancy rate at day 27 was negatively affected by ovulatory follicle size ($r = -0.17$). The positive effects of estradiol and progesterone were independent and likely aid in the establishment of a maternal environment that is conducive to pregnancy establishment (Inskeep 2004). The negative effect of ovulatory follicle size on pregnancy rate was unexpected. Since ovulatory follicle size had a negative effect on stage of embryonic development, the negative effect of ovulatory follicle size may reflect an inability of the embryo to produce the signal for maternal recognition of pregnancy before the onset of luteolysis.

Mechanisms Associated With Pregnancy Maintenance

GnRH-induced ovulation of small dominant follicles resulted in increased late embryonic/early fetal mortality in postpartum beef cows (Perry et. al., 2005). The majority of the preceding late embryonic/fetal loss occurred around the time of embryo uterine attachment (day 27 to 41; Inskeep 2004). This is a time when late embryonic/early fetal mortality has been reported by others (Table 1) and might be due to improper placentation. In the RET study, pregnancy maintenance was directly affected by embryo quality (r = 0.19) and recipient cow age (r= 0.14). Consequently, late embryonic/fetal mortality was associated with poorer quality embryos and younger cows. A positive association between embryo quality and pregnancy rates has been reported previously (Donaldson, 1985; Hasler, 2001).

Development of a method for predicting cows that have an increased probability of experiencing late embryonic/fetal mortality would be useful. Bovine pregnancy associated glycoproteins (bPAGs) are expressed in binucleate trophoblast cells of the placenta and can be detected in the maternal circulation beginning around days 24 to 26 of gestation (Figure 3; Pohler et. al., 2010). The bPAG family has been used to diagnose pregnancy and monitor embryonic/fetal viability as well as placental function in cattle. In the RET study, cows destined to undergo late embryonic or early fetal loss had significantly decreased bPAGs on day 28 of gestation even though all cows had a viable fetus, based on presence of a heartbeat (Figure 4). These data suggest that serum bPAGs at day 28 may be used to diagnosis pregnancy establishment and predict embryonic/fetal survival until at least d 72 of gestation, which accounts for the most susceptible time of embryonic or fetal mortality.

Summary

In cattle, fertilization generally occurs following > 90% of inseminations, but pregnancy rate at the earliest possible detection (day 27) is generally < 70%. Cows induced with gonadotropin releasing hormone (GnRH) to ovulate smaller follicles have reduced pregnancy rates and experience greater embryonic loss, even after pregnancy has been established. These inefficiencies are likely due to either ovulation of an immature oocyte that compromises fertilization and embryo survival or ovulation occurs before the follicular cells have fully matured to produce sufficient estradiol during the preovulatory period and subsequently, progesterone to adequately prepare the uterus for pregnancy. In this paper we describe a

reciprocal embryo transfer study that was designed to differentiate between follicular effects on oocyte quality and uterine environment on pregnancy success in beef cattle. We used path analysis to describe relationships among the complex array of factors affecting pregnancy success. Follicular environment of the donor cow affected fertilization rate and embryonic survival prior to day 7 but survival after day 7 was primarily dependent on ovulatory follicle size, estradiol production, and subsequent progesterone production in the recipient cows, and largely independent of donor cow effects. The data provided in this paper demonstrate the numerous variables that contribute to successful establishment of pregnancy. Increased estradiol at the time of insemination in cattle and probably all species is critically important to fertility and embryo survival.

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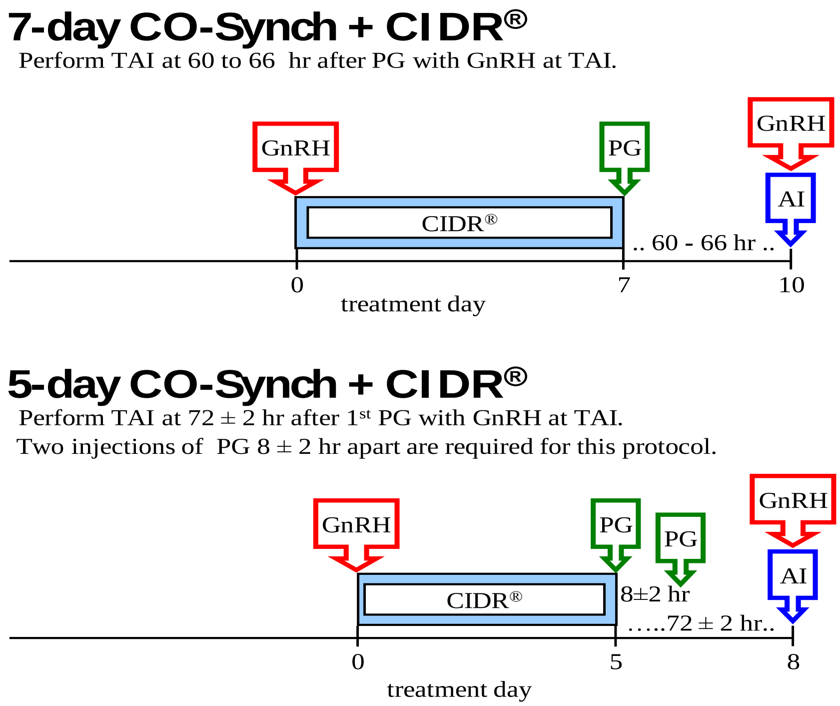

Figure 1. Current recommended methods for fixed-timed insemination (FTAI) in beef cows. . GnRH = gonadotropin releasing hormone; PG = prostaglandin $F_{2\alpha}$; CIDR – controlled internal drug release; and AI = artificial insemination.

Figure 1.

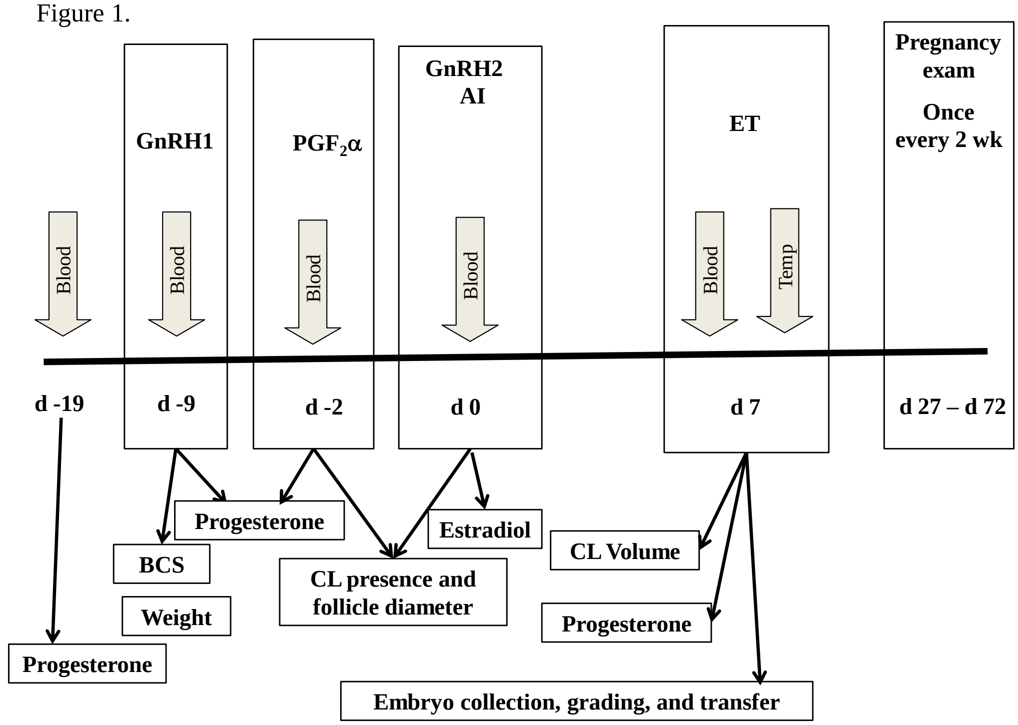

Figure 2. Experimental design. Treatments were based on ovulatory follicle size at GnRH2 of the donor and recipient cows. Embryos collected from cows that ovulated a small follicle (<12.5 mm) or large follicle (≥12.5 mm) were transferred into recipients that ovulated a small or large follicle resulting in the following treatment groups: small to small (n = 71; negative control), small to large (n = 111; examine effect of oocyte competence), large to small (n = 122; examine effect of maternal environment), and large to large (n = 50; positive control). Includes data on 1,164 single ovulations in suckled beef cows that were treated with the CO-Synch protocol (GnRH1 on day -9, $PGF_{2\alpha}$ on day -2, and GnRH2 with [donor cows; n = 810] or without [recipient cows; n = 354] fixed timed artificial insemination [AI] at day 0). Embryo collection, grading, and transfer (ET) occurred 7 days after GnRH2 administration. Pregnancy diagnosis began on day 27 to 29 (day 0 = GnRH2) and continued every other week until day 72 to 74. Blood = blood collection for quantification of serum concentrations of progesterone and estradiol, Temp = rectal temperature, BCS = body condition score.

Table 1. Late embryonic/fetal morality in beef heifers and lactating beef cows

Beef Cattle	Number of pregnancies	Days of gestation at diagnosis		Interval (days)	Pregnancy loss (%)	Reference
		First	Second			
Heifers	149	30	60	30	4.0	Lamb (2002)
Heifers	271	35	75	40	4.1	Lamb (2002)
Heifers	105	30	90	60	4.8	Lamb (2002)
Overall	525	30-35	60-90	30-60	4.2 (4.1-4.8)	
Lactating						
Cows	138	25	45	20	6.5	Beal et al. (1992)
Cows	138	25	65	40	8.0	Beal et al. (1992)
Cows	223	29-33	54-61	~26	10.8	Stevenson et al. (2003)
Overall	361	25-33	45-65	20-40	8.8 (6.5-10.8)	

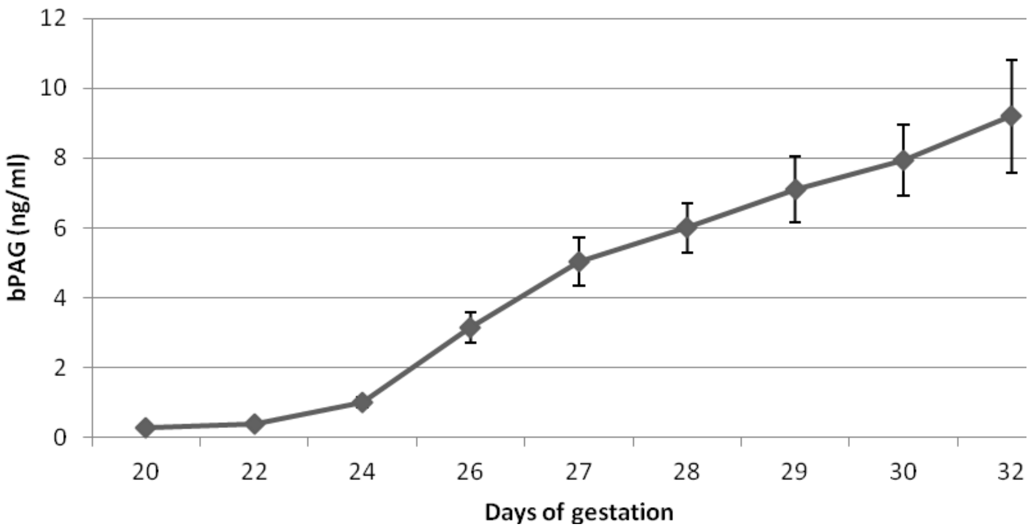

Figure 3. Serum concentrations of bPAGs from artificial insemination (day 0) to day 32 of gestation. First significant increase ($P < 0.0001$) in circulating bPAG concentrations occurred on day 24 of gestation.

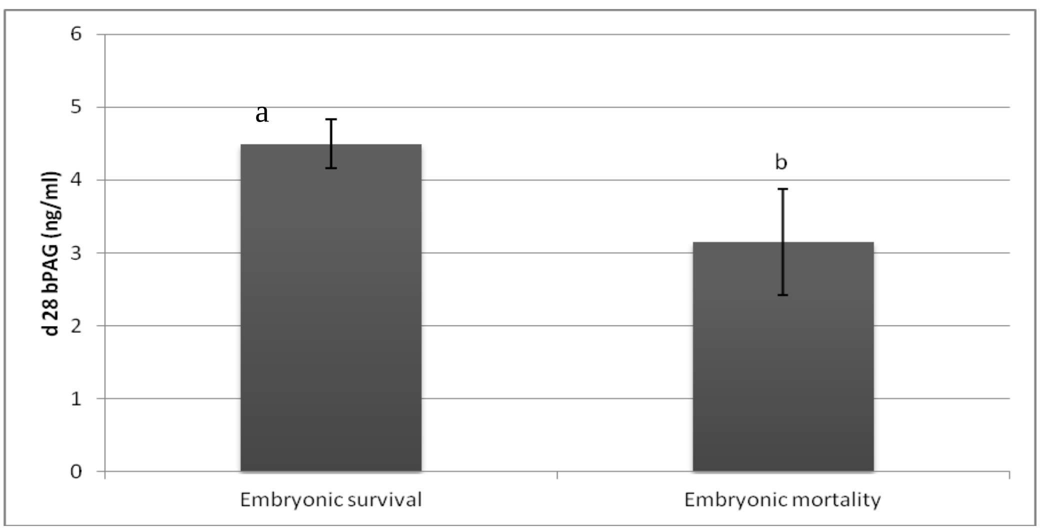

Figure 4. Serum concentrations of bPAGs in postpartum beef cows that had a viable embryo on day 28 (n = 195) and either maintained pregnancy (Embryonic survival; n = 176) or did not maintain pregnancy (Embryonic mortality; n = 19). Cows that experienced embryo mortality by day 72 had lower serum concentrations of bPAGs on day 28 compared to cows that maintained an embryo until day 72 ($P < 0.05$).