



**ARIZONA AND NEW MEXICO
DAIRY NEWSLETTER**

**COOPERATIVE EXTENSION
The University of Arizona
New Mexico State University**

March 2009

THIS MONTH'S ARTICLE:

**Metabolic Adaptations to Heat Stress and Related
Effects on Fertility**

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**Reprinted from the Southwest Nutrition and Management Conference Proceedings
Phoenix, Arizona
February 2009**

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**Arizona Dairy Production Conference
Hilton Garden Inn
Phoenix, AZ
October 8, 2009**

Metabolic Adaptations to Heat Stress and Related Effects on Fertility

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SUMMARY

- During periods of heat stress, dairy cattle employ numerous metabolic adaptations in order to survive.
- Several of these metabolic adaptations interfere with reproductive performance and contribute to decreased conception rates (including increased circulating ghrelin and plasma urea nitrogen concentrations).
- Ghrelin is a hormone involved in feed intake regulation that increases during periods of heat stress in dairy cattle.
- Elevated ghrelin concentrations are associated with decreased reproductive performance in rodents, and are likely to have similar effects in dairy cattle.
- Plasma urea nitrogen concentrations also increase during periods of heat stress in dairy cattle (irrespective of changes in diet formulation or intake).
- High plasma urea nitrogen concentrations are associated with decreased fertility in lactating dairy cows.

INTRODUCTION

The physiological effects of heat stress on the productivity of dairy cattle are financially devastating for the dairy industry. These physiological effects have been described in excellent reviews by Beede and Collier (1986) and West (1999). During periods of heat stress, dry matter intake (DMI) decreases and maintenance requirements increase as cattle attempt to dissipate excess heat load (West, 1999). In addition, changes in blood flow and the production of various hormones ultimately result in decreased reproductive performance and milk production: two economically vital aspects of dairy production. During summer months, conception rates can decline 20-30% (Rensis and Scaramuzzi, 2003). This observed reduction in fertility, is attributed to several factors, including early embryonic death, inhibition of follicular dominance, and reduced ovarian steroidogenic output (Putney et al., 1988; Rensis and Scaramuzzi, 2003; Wolfenson et al., 2000). Thus, heat stress has a wide range of reproductive effects beginning with the oocyte in the developing follicle and continuing through early embryonic development. The biological mechanisms that mediate these effects, however, are not completely understood. In this discussion, we will focus on two factors we are investigating that affect reproductive performance during periods of heat stress: changes in ghrelin secretion and the implications of elevated concentrations of plasma urea nitrogen (PUN).

GHRELIN

A hormone that is likely involved in the observed decrease in reproduction during periods of heat stress is ghrelin. Ghrelin is a 27-amino acid peptide (bovine) that is primarily secreted from the lining of the stomach. Though it was first identified as a growth hormone secretagogue, a complete understanding of ghrelin's vast array of physiological influences remains to be elucidated (Kojima et al., 1999). Research has clearly shown, however, that ghrelin is a potent regulator of feed intake. The active ghrelin receptor, GHSR1a, has been identified in hypothalamic neurons containing proteins associated with feed intake regulation (neuropeptide-Y and agouti-related protein; Kojima and Kangawa, 2005; Korbonits et al., 2004). Furthermore, ghrelin administration increases the feed intake of rodents (Wren et al., 2000) and endogenous ghrelin secretion increases with feed restriction (Hayashida et al., 2001). Similar observations have been made in cattle. Following ghrelin administration, the feed intake of beef steers increased within one hour post-injection (Wertz-Lutz et al., 2006). Likewise, ghrelin concentrations are elevated in nutrient-restricted steers and in early-lactation dairy cows experiencing a state of negative energy balance (Bradford and Allen, 2008; Wertz-Lutz et al., 2008). Circulating ghrelin concentrations also change during the peri-prandial period in cattle, with ghrelin concentrations decreasing following feeding (Miura et al., 2004; Wertz-Lutz et al., 2006).

Implications for Fertility During Periods of Heat Stress

During periods of heat stress, mean plasma ghrelin concentrations increase in early lactation dairy cattle (Figure 1; Field et al., unpublished); likely resulting from decreased DMI. Reproductively, the increase in circulating ghrelin concentrations is significant because rodent studies have shown that when ghrelin increased in the circulation, it was also elevated in the secretions of the reproductive tract (perhaps to an even greater extent than in plasma; Kawamura et al., 2003). During embryo culture, ghrelin significantly decreased embryonic development and viability. Furthermore, rodents with elevated circulating concentrations of ghrelin (either by exogenous ghrelin injection or underfeeding) experienced decreased embryonic development and increased embryonic loss (Barreiro and Tena-Sempere, 2004). Taken together, this evidence suggests that as circulating ghrelin concentrations increase during periods of heat stress in dairy cattle, embryonic development and survival is directly compromised.

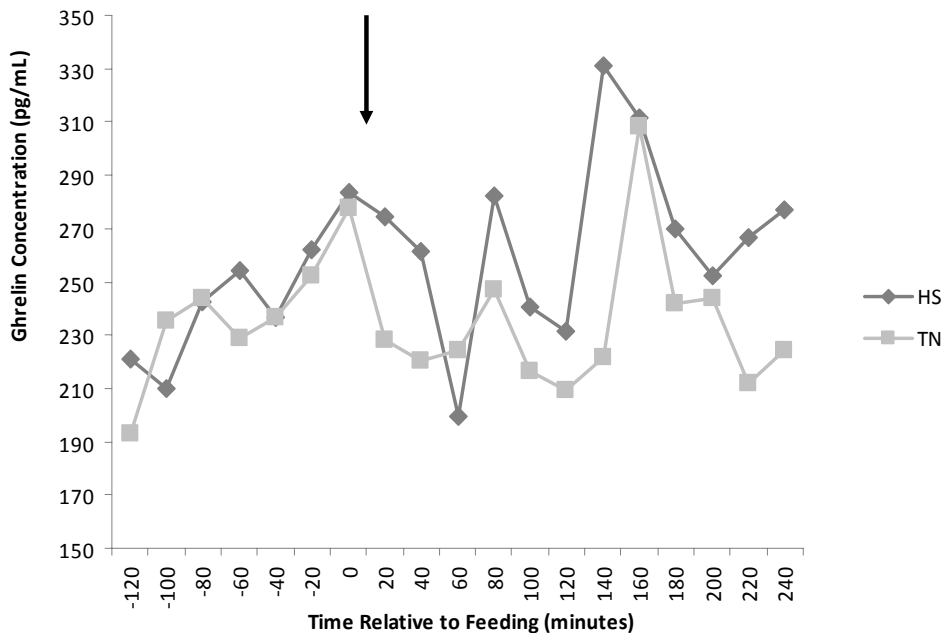


Figure 1. Mean plasma ghrelin concentrations in heat stressed (HS) and thermal-neutral (TN) cows. Arrow indicates time point when feed was given. Plasma ghrelin was greater in HS than TN cows ($P < 0.05$; Field et al., unpublished).

HEAT STRESS AND PLASMA UREA NITROGEN

As dairy cattle digest a ration, amino acids from the diet are metabolized to ammonia in the rumen which is then either converted to microbial protein or absorbed into the blood stream. Circulating ammonia is quickly converted to urea by the liver, after which it can be either excreted or recycled (Van Soest, 1994; Visek, 1984). Conditions resulting in elevated PUN levels have been linked to decreased fertility in most (Blanchard et al., 1990; Butler et al., 1996; Canfield et al., 1990; Ferguson et al., 1993; Jordan and Swanson, 1979; Kaim et al., 1983) studies dealing with feeding high protein diets to dairy cattle.

For reasons that are not yet understood, heat stress is one condition that increases circulating PUN concentrations. This phenomenon may be a consequence of increased skeletal muscle breakdown rather than protein metabolism. An indicator of muscle catabolism is 3-methyl-histidine, which is reported to increase in heat-stressed poultry, and is independent of reduced DMI (Yunianto et al., 1997). Direct effects of heat stress on muscle breakdown (3-methyl-histidine or creatine) have been reported in exercising men (Febbraio, 2001), rabbits (Marder et al., 1990) and lactating cows (Kamiya et al., 2006; Schneider et al., 1988). Other factors that may contribute are increased digestibility of the diet (due to decrease passage rate; West, 1999) and decreased blood flow to the kidneys for excretion of urea (Kenney and Musch, 2004; Lee et al., 2005). The end result of these physiological changes that occur during heat stress is

elevated PUN concentrations in heat-stressed cows irrespective of changes in diet formulation or declining DMI. The rise in PUN concentrations during periods of heat stress has been described in two separate studies where diet formulation was the same for cows in thermal-neutral and heat stress conditions. In a study conducted by Wheelock et al. (unpublished) the PUN concentrations of pair-fed cows in thermal-neutral conditions were compared to those of heat-stressed cows and in another study conducted by Settivari et al. (2007) PUN concentrations were measured as cows transitioned from thermal-neutral to heat stress conditions. Both experimental designs resulted in significantly increased PUN concentrations during heat stress.

Implications for Fertility

The conception rates of both dairy cows and heifers have been shown to plummet dramatically in response to elevated PUN concentrations. During these studies, when PUN levels exceeded 19 or 20 mg/dL there was approximately a 20 percentage point decrease in conception rates (Butler et al., 1996; Elrod and Butler, 1993; Ferguson et al., 1988; Ferguson et al., 1993). Such a significant decrease in conception rates represents a large economic loss to dairy producers.

Reproductive processes that are likely to be affected by excess PUN concentrations include follicular, luteal and embryonic development. Therefore, previous research has focused primarily on direct detrimental effects of PUN on the gametes (especially the oocyte), embryonic development and survival and progesterone production and secretion. Discrepancies in the results of these studies have fostered a debate amongst scientists concerning the true impact of excess PUN on fertility. Clearly, however, high PUN values have a dramatic effect on reproduction in most (but not all) cases. The key to these discrepancies may be a synergistic interaction with the early lactation cow's physiological state (especially heat stress and negative energy balance).

Circulating concentrations of urea equilibrate within reproductive fluids and increase proportionally with increasing concentrations of PUN. For example, follicular fluid urea concentrations (Hammon et al., 2005; Leroy et al., 2004) are highly correlated with PUN concentrations during early lactation (r^2 values between 0.61 and 0.98) suggesting that the oocyte within the developing follicle is susceptible to damage by high PUN concentrations. Indeed, a recent study found that follicular fluid urea nitrogen concentrations (and presumably PUN concentrations) were a predictor of the developmental competence of bovine oocytes. Following fertilization, the embryos from the higher urea nitrogen oocytes had lower cleavage and blastulation rates (Iwata et al., 2006). Thus, the oocytes that encounter elevated urea concentrations within the follicular fluid are less likely to develop into competent, viable embryos. This data is particularly disconcerting because it takes over 30 days for ovarian follicles to progress from initial antrum formation to recruitment (Mihm and Bleach, 2003), presenting a significant window of time during which the oocyte is susceptible to damage.

Likewise, the concentrations of urea are higher in the uterine fluid of cows with greater PUN concentrations. Urea concentrations within the uterine fluid were higher both at estrus and during the luteal phase. High concentrations of PUN within the uterus during the luteal phase suggest that urea may act directly on the embryo to decrease development and viability. Indeed, the direct effect of urea on embryonic development has been demonstrated *in vitro*. Embryos that were cultured in media containing 21 mg of urea/dL were more likely to degenerate before they reached the blastocyst stage than those cultured in control media (Ocon and Hansen, 2003).

The results of these experiments indicate that the uterine environment of dairy cattle with high PUN concentrations is suboptimal for embryonic development and may be one of the primary factors contributing to the observed decrease in fertility.

Elevated urea concentrations within the uterus may also indirectly affect embryonic development and survival by altering the uterine environment (especially secretory activity). Many of the changes that have been observed in the uterine environment in response to high PUN concentrations are occurring at a time during the estrous cycle when a functional corpus luteum is present and the embryo has migrated to the uterus (Elrod and Butler, 1993; Elrod et al., 1993). Therefore, these changes have the potential to significantly affect the fertility of cows with elevated PUN concentrations.

Even seemingly minor alterations in the uterine milieu can be catastrophic for developing embryos. Previous research has shown that the uterine environment of dairy cows is indeed affected by PUN concentrations, particularly during the luteal phase. For example, ion concentrations (P, Mg, K and Zn) differed within the uterine fluid between cows fed diets containing relatively high or low protein concentrations (Jordan et al., 1983). In another study, similar changes in ion concentrations within uterine flushings were associated with the production of abnormal embryos that would be less likely to continue developing and survive (Wiebold, 1988).

The uterine luminal pH of cows fed high protein diets is also affected by circulating PUN concentrations. Both cows and heifers fed high protein diets (resulting in high PUN concentrations) had lower uterine pH values 7 days after estrus (luteal phase) than the animals fed the control diets (Elrod and Butler, 1993; Elrod et al., 1993). Interestingly, there were no differences in uterine pH at estrus regardless of diet. Based on these results, Rhoads and co-workers (2004) directly infused urea or saline (control) into the circulation during the luteal phase. Mean PUN concentrations increased from 16.6 mg/dL to 22.6 mg/dL during urea infusion. Uterine pH remained relatively constant during saline infusion but decreased during urea infusion (Figure 2; from 7.08 at 6 hours to 6.88 at 18 hours of infusion). During embryo culture, lowering the pH of the culture media to similar levels reduced cleavage rates and almost completely inhibited the development of embryos to the blastocyst stage (Ocon and Hansen, 2003). Thus, even the minor changes in uterine luminal pH that are observed in association with high PUN concentrations are capable of decreasing embryo viability.

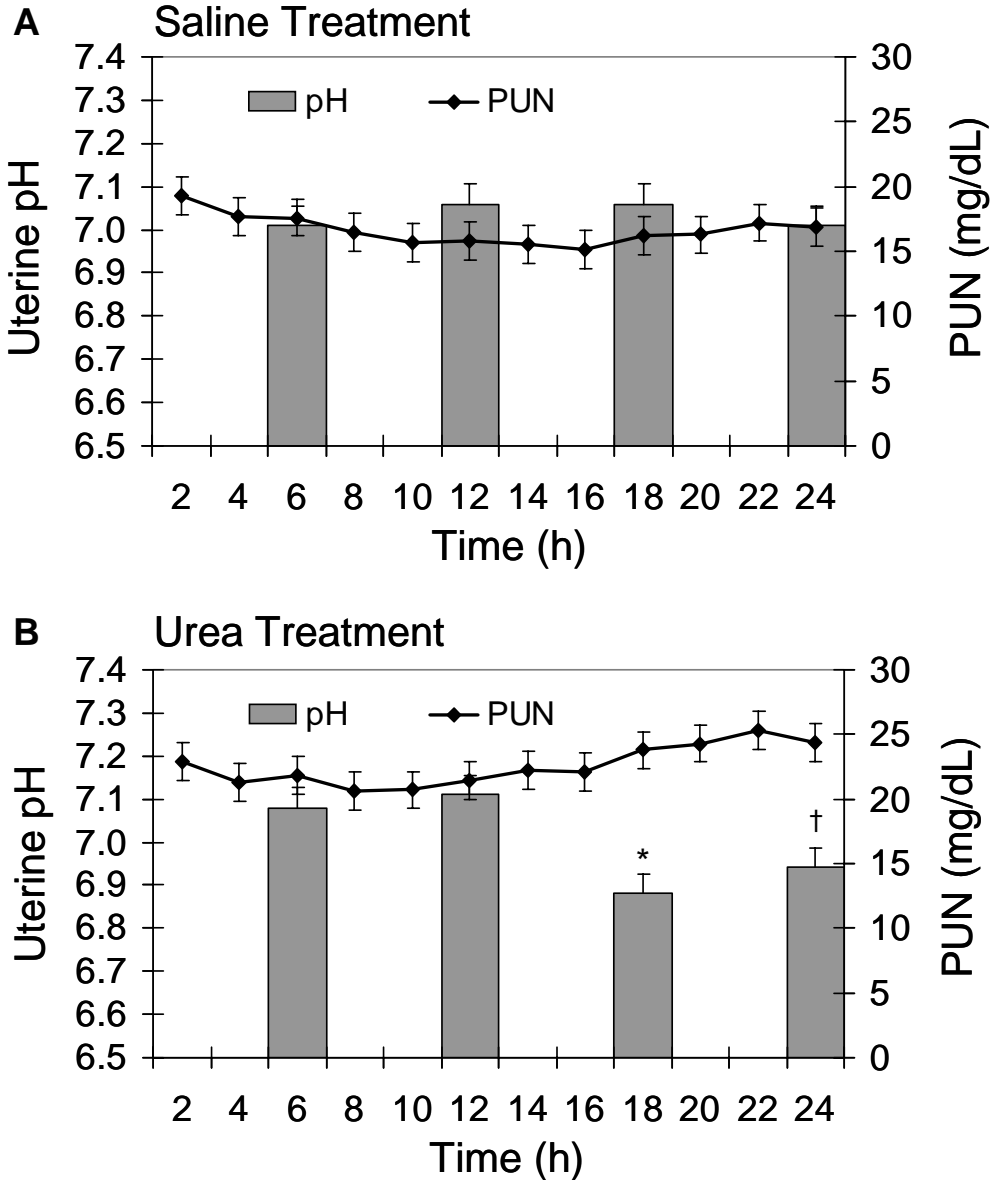


Figure 2. Least-squares means and standard errors for plasma urea nitrogen (PUN) concentrations and uterine pH during intravenous infusion of saline (panel A; n=8) and urea (panel B; n=8) in lactating dairy cows. (A) Uterine pH was not significantly affected by saline infusion. (B) A treatment × time interaction was detected for uterine pH. *Uterine pH at 18 h differed ($P < 0.05$) from those at 6 and 12 h. †Uterine pH at 24 h tended ($P = 0.09$) to differ from that at 12 h (Rhoads et al., 2004).

Likewise, previous investigations have revealed decreased embryonic survival both *in vivo* and *in vitro* when embryos were collected from ewes fed high levels of protein. In addition to decreased embryo recovery rates and decreased pregnancy rates, embryos that were collected from donor ewes consuming high levels of urea were less likely to develop to the blastocyst stage in culture (Bishonga et al., 1996). Embryos from ewes consuming high urea diets also used more glucose at embryo collection, and after culture, some experienced up to a 2.8-fold increase in metabolic rate (McEvoy et al., 1997). The availability of nutrients to the embryo that would be needed to support such an accelerated metabolic rate may be a factor contributing to the observed decrease in embryo survival. While these studies were conducted with sheep rather than dairy cows, they clearly demonstrate a dramatic impact on embryo development and viability.

When bovine embryos were evaluated by Blanchard et al. (1990), no differences were found in mean number of fertilized, unfertilized, transferable or nontransferable ova from lactating cows fed either a 73 or 64% rumen degradable intake protein (DIP) diet. However, more fertilized ova were recovered from cows fed the lower DIP diet. Cows on the lower DIP diet also tended to have a higher proportion of transferable ova and more of the cows fed the high DIP diet failed to yield transferable ova.

In another study, bovine embryos from superovulated, non-lactating cows on low and high protein diets were evaluated. Visual, microscopic and staining techniques were used to assess the characteristics of embryos from cows with mean PUN levels of 9.8 mg/dL (low protein diet) and 21.3 mg/dL (high protein diet). No quantitative or qualitative differences were observed between the two treatment groups (Garcia-Bojalil et al., 1994). However, appearances can be deceiving. Rhoads and co-workers (2006) collected embryos from lactating dairy cows consuming diets designed to result in either high (24.4 mg/dL) or moderate (15.5 mg/dL) PUN concentrations and transferred them to heifers also consuming two levels of dietary protein (resulting in PUN concentrations of 7.7 and 25.2 mg/dL). In agreement with previous studies, they also failed to observe any differences in the quantity or quality of embryos collected from the two experimental groups (Table 1). However, following transfer, differences in embryo viability became apparent. The transfer of embryos collected from the high PUN donors resulted in fewer pregnancies than the embryos collected from moderate PUN donors (Table 2; 11 vs. 35% pregnancy rate). Interestingly, there were no differences in pregnancy rate based on the PUN concentrations of the recipient animals. Since pregnancy rates were only affected by the PUN concentrations of the donor animals, we can conclude that either the oocyte or embryo was damaged by high PUN concentrations on or before day 7 of pregnancy (the day that embryos were collected from donors), resulting in decreased long-term viability.

Table 1. Morphological evaluation and numbers of embryos recovered from donor lactating cows with moderate or high plasma urea nitrogen (PUN; Rhoads et al., 2006).

Characteristic	Donor Cow Group		
	Moderate PUN	High PUN	
Grade ^a	1	40	49
	2	1	6
	3-5	3	6
	6	6	5
Stage ^b	4	30	47
	5	6	5
	6	5	3

^a Grade 1 = excellent, Grade 2 = good, Grade 3-5 = fair to very poor, Grade 6 = unfertilized oocyte. Embryos grading ≥ 3 were not transferred to recipient heifers.

^b Stage 4 = compact morula, Stage 5 = early blastocyst, Stage 6 = blastocyst.

Table 2. Pregnancy rates achieved following transfer of embryos from donor cows with high or moderate plasma urea nitrogen (PUN) concentrations into high or low PUN recipient heifers. The data is number of pregnancies/number of transfers with pregnancy rate % in parentheses (Rhoads et al., 2006).

	High Donor	Moderate Donor	Total
High Recipient	3/18 (17%)	4/12 (33%)	7/30 (23%)
Low Recipient	2/27 (7%)	9/25 (36%)	11/52 (21%)
Total	5/45 (11%) ^a	13/37 (35%) ^b	

^{a, b} Values are significantly different ($P < 0.02$).

CONCLUSIONS

Dairy cattle are forced to employ numerous metabolic adaptations in an attempt to maintain homeothermy during periods of heat stress. Unfortunately, many of these adaptations are detrimental to reproductive performance. Two examples include increased circulating concentrations of ghrelin and PUN. We do not yet understand precisely how elevated ghrelin and PUN affect fertility, although it is apparent that they both have devastating consequences for early embryonic development. Ongoing research is committed to elucidating the mechanisms responsible for decreased reproductive performance in the presence of ghrelin and PUN. Results of these experiments will provide the knowledge we need to develop strategies for ameliorating the economic impact of heat stress on reproduction in dairy cattle.

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HIGH COW REPORT

February 2009

MILK

Arizona Owner	Barn#	Age	Milk	New Mexico Owner	Barn #	Age	Milk
*Dutch View Dairy	671	04-01	35,920	*North Star Dairy Llc	2966	4-03	38,840
*Goldman Dairy	4166	05-03	33,660	*Providence Dairy	7117	5-01	37,410
*Dutch View Dairy	207	04-01	32,960	*North Star Dairy Llc	2265	5-06	37,190
*Stotz Dairy	21714	04-08	32,790	Pareo Dairy	5425	5-01	37,034
*Stotz Dairy	2,173	03-05	32,490	*Do-Rene Dairy	4715	6-06	36,070
*Goldman Dairy	5106		32,490	*Providence Dairy	7207	5-01	35,510
Lunts Dairy	5716	04-00	32,350	*North Star Dairy Llc	2152	6-06	35,470
*Stotz Dairy	23478	03-03	32,350	*North Star Dairy Llc	3256	4-03	35,330
*Goldman Dairy	1032		31,740	Pareo Dairy	4866	6-09	35,181
*Paloma Dairy	2024	04-03	31,670	*Providence Dairy	3350	-----	35,130

FAT

*Paloma Dairy	322	05-04	1,308	*Goff Dairy	6963	4-03	1,402
Lunts Dairy	5871	03-04	1,292	Mccatharn Dairy	2417	7-04	1,332
*Stotz Dairy	21603	04-10	1,277	*Tee Vee Dairy	1590	6-06	1,329
*Rio Blanco Dairy	7817	04-05	1,256	*North Star Dairy Llc	2152	6-06	1,325
*Stotz Dairy	21496	04-11	1,230	*North Star Dairy Llc	1676	6-06	1,309
*Stotz Dairy	21714	04-08	1,226	S.A.S. Dairy	9328	4-04	1,297
*Goldman Dairy	1032		1,201	Wayne Palla Dairy	-----	6-06	1,289
*Stotz Dairy	22248	04-04	1,181	*North Star Dairy Llc	2265	5-06	1,263
*Stotz Dairy	22488	04-02	1,177	*North Star Dairy Llc	12264	5-06	1,262
*Stotz Dairy	21790	04-07	1,173	*North Star Dairy Llc	2698	5-06	1,242

PROTEIN

*Dutch View Dairy	671	04-01	1,033	*North Star Dairy Llc	2152	6-06	1,258
*Goldman Dairy	5106		1,014	*North Star Dairy Llc	2265	5-06	1,104
*Stotz Dairy	21714	04-08	992	*North Star Dairy Llc	2031	6-06	1,088
Lunts Dairy	5716	04-00	971	*North Star Dairy Llc	2966	4-03	1,086
*Stotz Dairy	23327	03-04	962	*North Star Dairy Llc	3332	4-03	1,086
*Dutch View Dairy	207	04-01	958	*Stark Everett Dairy	7081	4-03	1,082
Lunts Dairy	5441	05-04	956	*North Star Dairy Llc	12712	3-04	1,080
Lunts Dairy	5641	04-04	946	Red Roof Dairy	7063	5-00	1,074
*Goldman Dairy	4166	05-03	924	*North Star Dairy Llc	12252	3-04	1,068
*Stotz Dairy	21496	04-11	917	*North Star Dairy Llc	3153	4-03	1,063

*all or part of lactation is 3X or 4X milking

**ARIZONA - TOP 50% FOR F.C.M.^b
February 2009**

<u>OWNERS NAME</u>	<u>Number of Cows</u>	<u>MILK</u>	<u>FAT</u>	<u>3.5 FCM</u>	<u>CI</u>
*Stotz Dairy West	2,367	26,474	966	27,113	15
*Goldman Dairy	2,399	25,166	866	24,925	14
*Danzeisen Dairy, Inc.	1,694	24,511	874	24,772	14
*Riggin Ranch	1,162	25,040	847	24,562	13
*Stotz Dairy East	966	23,390	846	23,834	14
*Shamrock Farms	8,210	24,640	808	23,756	14
*Zimmerman Dairy	1,250	23,019	808	23,057	14
*Withrow Dairy	5,187	23,038	805	23,016	13
Paul Rovey Dairy	253	22,716	804	22,861	14
Lunts Dairy	723	22,134	814	22,772	13
Parker Dairy	4,373	22,008	782	22,198	15
*Saddle Mountain	3,062	21,601	792	22,184	14
*Rio Blanco Dairy	2,131	20,232	822	22,080	14
*Mike Pylman	6,628	22,394	761	22,024	16
*Cliffs Dairy	338	20,774	776	21,568	14
*DC Dairy, LLC	1,128	21,396	754	21,474	
*Yettem	3,686	17,985	838	21,361	
*Shamrock Farms Emerald	18	20,264	764	21,153	16
*Dutch View Dairy	2,392	20,704	703	20,352	15
*Jal Dairy	18	16,757	803	20,271	13

**NEW MEXICO - TOP 50% FOR F.C.M.^b
February 2009**

<u>OWNERS NAME</u>	<u>Number of Cows</u>	<u>MILK</u>	<u>FAT</u>	<u>3.5 FCM</u>	<u>CI</u>
*Pareo 2	1,691	24,774	913	25,517	13.50
*SAS	1,978	24,288	915	25,340	13.10
McCatharn	1,135	24,985	891	25,252	13.30
*Butterfield	2,260	26,420	830	24,883	13.30
*Clover Knolls	3,499	25,011	844	24,501	12.90
*Milagro	3,481	23,801	874	24,464	13.82
*Do-Rene	2,411	24,794	827	24,132	12.00
*Vaz	2,130	23,164	859	23,946	14.70
Vaz 2	1,969	22,942	857	23,817	14.00
*Providence	3,313	23,348	824	23,458	13.30
*Goff	6,033	24,421	785	23,289	13.30
*Tee Vee	1,137	22,504	821	23,044	14.12
Cross Country	3,856	22,336	819	22,939	13.00
*Tallmon	539	21,911	830	22,934	13.70
Stark Everett	3,204	22,689	808	22,913	13.50
Ridgecrest	3,911	22,297	796	22,549	12.60
*Pareo	3,724	22,246	794	22,495	13.50

* all or part of lactation is 3X or 4X milking

^b average milk and fat figure may be different from monthly herd summary; figures used are last day/month

ARIZONA AND NEW MEXICO HERD IMPROVEMENT SUMMARY FOR OFFICIAL HERDS TESTED February 2009

		ARIZONA	NEW MEXICO
1.	Number of Herds	29	24
2.	Total Cows in Herd	62,349	59,291
3.	Average Herd Size	2,150	2,470
4.	Percent in Milk	88	87
5.	Average Days in Milk	193	202
6.	Average Milk – All Cows Per Day	60.9	65
7.	Average Percent Fat – All Cows	3.6	3.62
8.	Total Cows in Milk	55,848	51,583
9.	Average Daily Milk for Milking Cows	67.9	70.08
10.	Average Days in Milk 1st Breeding	87	76.56
11.	Average Days Open	154	148
12.	Average Calving Interval	14.3	14.13
13.	Percent Somatic Cell – Low	84	83
14.	Percent Somatic Cell – Medium	12	13
15.	Percent Somatic Cell – High	4	4
16.	Average Previous Days Dry	63	62
17.	Percent Cows Leaving Herd	34	34
Milk		21,269	19,897
Percent butterfat		3.63	3.61
Percent protein		3.06	3.13
Pounds butterfat		770	846
Pounds protein		649	703



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SAVE THE DATE

Arizona Dairy Production Conference
Hilton Garden Inn
Phoenix, AZ
October 8, 2009

