Recent Advances in Amino Acid and Energy Nutrition of Prolific Sows** - Review -

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ABSTRACT : Prolific females require better nutrition and feeding practice because of larger litter size and the substantial decline in body fat. Life-time pig output will be compromised if body protein and fat are not properly managed. First litter females are especially vulnerable because they can loose ≥15% of whole-body protein. Conservation of body protein mass during first lactation minimizes wean to estrus interval and increases second litter size (up to 1.2 pigs). The ability to influence litter-size by amino acid nutrition is a new dimension in our understanding. A P_2 fat depth below 12 mm at farrow and below 10 mm at wean compromised wean to estrus interval (>2 d) and next litter size (0.5 to 1.5 pigs) in sows. It is now clear that a 'modest' excess of feed during the first 72 h of pregnancy decreases embryo viability so that the potential for an increased litter size at birth is not realized. The capacity for milk production by prolific young sows is 25% higher than the standard used previously (NRC, 1988). First litter females averaged 9.82 kg milk/d for a 21 d lactation. Second and third litter counterparts averaged 10.35 kg/d. Milk production was 95% of peak by 10 d of lactation and sows were in greatest negative energy and lysine balance during the first 6 d. Nearly 45% of the total loss in body protein occurred within the first 6 d, but this could reduced to 30-35% by using a more aggressive feeding strategy after parturition. There appear to be 2 phases in lactation for lysine need (d 2-12 vs 12-21). Feeding to the higher level alleviates the second litter size decline. The lysine requirement for lactation can be predicted with accuracy, but we are not able to predict the second limiting amino acid. Mammary uptake of valine relative to lysine and recent work with practical diets suggest that the recent NRC (1998) pattern is realistic and that threonine and valine could be co-limiting for corn-soy diets for prolific sows nursing 10-11 pigs. Empirical studies are needed to refine the ideal pattern so that synthetic lysine can be used with more confidence. Milk fat output for the elite sow is extraordinary and poses an unnecessarily high energetic cost. Methods that reduce mammary fat synthesis will benefit the sow and may enhance piglet growth. *(Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 11 : 1638-1652)*

Key Words : Sow, Nutrition, Pregnancy, Lactation, Amino Acids, Energy

INTRODUCTION

A high level of weaned pig output can be maintained over the reproductive life of the sow if she consumes adequate amounts of energy and nutrients. First litter females are especially vulnerable to nutrition deficit, which typically occurs during lactation. Adequate intake of amino acids during lactation is important for first litter females since excessive body protein loss results in a prolonged wean to estrus interval (WEI) and reduced subsequent litter size. A practical outcome of extended WEI is to cull for presumed reproductive failure. Severe and chronic depletion of body protein and fat reserves appear to compromise pig output in multiparous females. The impact on lifetime pig output can be significant if this goes uncorrected.

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A feeding strategy requires decisions on feed amount and nutrient level. The two major issues in program design are: (1) setting proper endpoints for body size and condition and, (2) setting feed and nutrient level to match sow endpoints and litter gain. The challenge is to meet nutrient needs of a herd where sows differ in body size, body condition and stage of pregnancy. This paper reviews recent advances in the energy and amino acid nutrition of the prolific sow. It places them in the context of a practical feeding strategy with the objective of maximum lifetime pig output at a responsible dietary input cost.

IMPACT OF NUTRITION ON REPRODUCTION

Three examples are provided to illustrate how nutrition constrains the expression of genetic potential for reproduction. They are particularly relevant to modern prolific females since they produce more milk and have less body fat at breeding. Excessive body protein and fat loss during lactation results in a prolonged WEI and reduced second litter size. Second litter and older females are less able to have prolonged WEI because of their body size. However, extensive depletion of body reserves can also be detrimental to both WEI and future litter size.

Conservation of body protein and fat

Example 1: King (1987) observed that increases in body protein loss during lactation was associated with extended WEI in first litter sows (figure 1). There was a closer relationship between body protein loss and WEI (r^2=0.63) than between body fat loss and WEI (r^2=0.43). Thus, either absolute body protein mass, or the degree of protein loss exert a greater influence on days to rebreed than body fat. This argues against a strategy of nutritionally regulating growth for greater fat relative to protein gain in most females. The strategy should be to minimize body weight loss (r^2= 0.92 vs WEI) in first litter females, by proper feeding practice (Williams, 1998), and then to properly balance protein with litter growth rate and feed intake.

Example 2: Conservation of body protein mass during lactation in first litter females also appears to be important to second litter size. We observed a 1.2 pig increase in second litter size at the lysine intake (52 vs 32 g/d) that minimized muscle loss during first lactation (17 d; Touchette et al., 1998a). This confirmed a report by Tritton and co-workers (1996) who observed that first litter females fed 60 g lysine/d during a 28 d lactation had more pigs at next farrow when compared to sows receiving 28 to 45 g/d (figure 2). This response is important in light of the problem of a reduction (or plateau) in second litter size relative to the first. These studies introduced a new dimension for lactation amino acid research.

Example 3: We expect that a minimum body fat and protein mass (body condition) exists to support the genetic potential for litter size in multiparous sows. The status of body protein is difficult to assess in practice, however, body fatness can be estimated using affordable ultrasonic technology since fat tends to be deposited externally. Hughes (1993) reported that a P_2 fat depth below 12 mm at parturition and below 10 mm at weaning compromised the WEI (> 2 d) and next litter size (> 1.5 pigs) in second to sixth litter sows (table 1). We have information that supports this result on 250 multiparous sows (< 12 mm at breeding resulted in 0.40 pig/litter penalty; PIC Mexico, personal communication). This needs to be verified on a larger scale and with particular attention to whether this differs by parity or body size.

Quantitative fat depth measurement can be useful for establishing a herd profile. The objective should be to determine if (1) too many females are below a target minimum body condition (thin females tend to have low fat depth and an apparent loss of body muscle), and whether (2) too many females have more fat depth than necessary. We recommend that not more than 15% of the herd should have a P_2 fat depth below 12 mm. Establishing a herd profile that includes stage of reproduction is important to verify that the feed program is achieving body condition targets. Application of ultrasonic technology to individual sows to set feed level for fatness is not very reliable for reasons that will not be discussed here.

It is concluded that body reserves (protein, fat and bone) need to be conserved in first litter females and maintained above a critical minimum for multiparous sows. Life-time pig output can be compromised by (1) a reduction in second litter size by up to 1.2 pigs with (2) premature culling after the first litter being more likely with a prolonged WEI that is judged to be unacceptable. (3) Chronic body fat (and protein) depletion may reduce litter size in multiparous sows, if extensive, for each cycle that a sow is affected.

Body size and reproduction in first litter females

A complete reproductive cycle is one of the most nutritionally challenging activities that a female can undertake. The nutritional strategy prior to and during first pregnancy may also impact reproductive ability for first litter females since there appears to be a minimum body size needed to support a rapid return

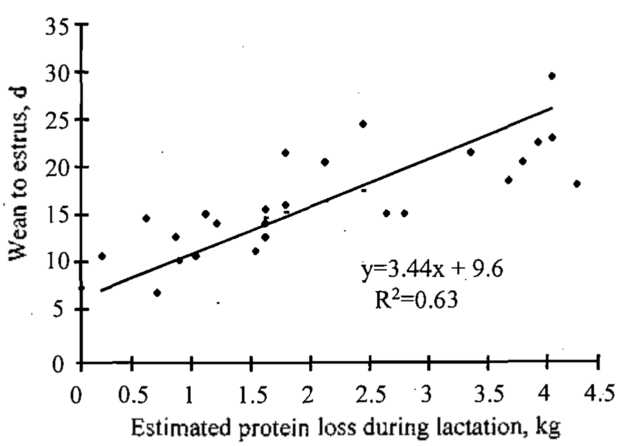

Figure 1. Estimated body protein loss during first lactation and wean to estrus interval (King, 1987)

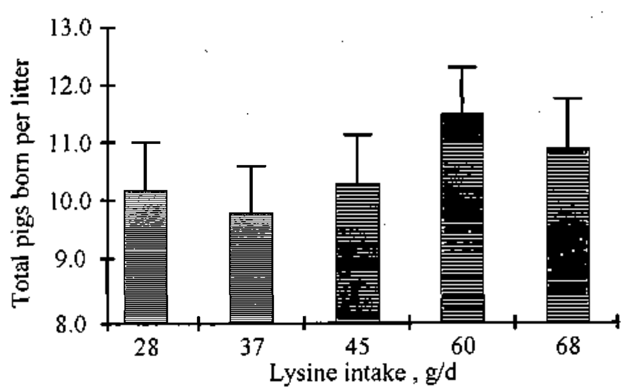

Figure 2. Impact of average dietary lysine intake during first lactation (28 d) and second litter total born (Tritton et al., 1996). Bars represent the SEM for each treatment.

to estrus. Williams and Mullan (1989) developed a relationship between female wean weight and WEI. Itsuggests that a wean weight of 150 kg or more minimizes wean to mating interval (figure 3) and that a progressive increase in the WEI is predictable. The insult of large protein and (or) fat losses to support lactation is greatest for young sows because their absolute body mass is low. This is illustrated later.

Dimensions of gilt development

Nutrition and development of the maiden female is important but beyond the scope of this review (see reviews by Whittemore, 1996 and Rozeboom, 1999). A number of studies have been conducted but few with modern genotypes. Proper development involves lifetime rearing to develop structural integrity and body mass. Bones of first litter sows are weaker and more vulnerable to fracture than older sows (Geissemann et al., 1998). Nutrition to optimize bone integrity of the maiden female should aim to maximize bone weight by the first two litters. Energy and amino acid nutrition should promote normal composition for the genetic type. Long-term immune acclimation to the herd is increasingly important in herds with significant pathogenic challenge.

Gilt development involves 3 periods: (1) growth to first litter, (2) first lactation feeding to minimize loss of body reserves, and (3) the rebuild of body protein, fat and bone reserves during the ensuing pregnancy. Conservation during first lactation followed by second pregnancy growth plus recovery of reserves are critical but generally ignored facets of female development.

The advantage of reduced growth rate prior to first breed on reproductive longevity has produced variable results. Restricted growth by feeding 2.3-2.6 kg of diet with adequate protein may be advisable if applied at puberty induction (about 150 d). This will slow growth slightly and may increase longevity (Rozeboom, 1999). The data suggesting a positive relationship between increasing body fatness and longevity 'merely reflect the consequences of subjecting improved pigs to conventional management' (Kirkwood, 1990). Kirkwood further states that 'when modern females are subjected to good management that minimizes body weight and condition during lactation, there is no association between...backfat depth at first successful breeding and subsequent reproductive performance.'

Table 1. Relationship between body fat depth at farrowing and the return to estrus interval and subsequent litter size in sows[a]

Fat depth, P_2 mm	Wean to extrus, d	Subsequent litter size	
		Total born	Born alive
Lactation, d 1			
<12	8.5	9.1	8.5
12 to 16	6.6	11.8	10.8
>16	6.1	12.0	10.3
Wean, d 27			
<10	8.1	9.9	8.9
10 to 13	6.7	11.1	9.9
>13	5.8	12.7	11.4

[a] 76 LW×LR sows (parity 2-6) with 9.5 pigs weaned. (Hughes, 1993).

FEEDING THE PREGNANT SOW

There are 3 stages of pregnancy that merit different feeding strategies. The first stage is early pregnancy and involves embryo survival and implantation (d 0-21). The second stage is devoted to body growth and reserves recovery. Sows are fed to support target maternal gains and to recover body reserves that were mobilized during the previous lactation. This is also the period when fetal muscle fiber numbers are established (d 20-80). These set the 'ceiling' for postnatal growth rate and efficiency (Stickland, 1994). The third phase is late pregnancy (last 35 d) and is characterized by exponential fetal and mammary growth. Our discussion will be restricted to recent advances and to proper feed levels for each stage.

Early pregnancy nutrition

Under-nutrition in early pregnancy has to be very

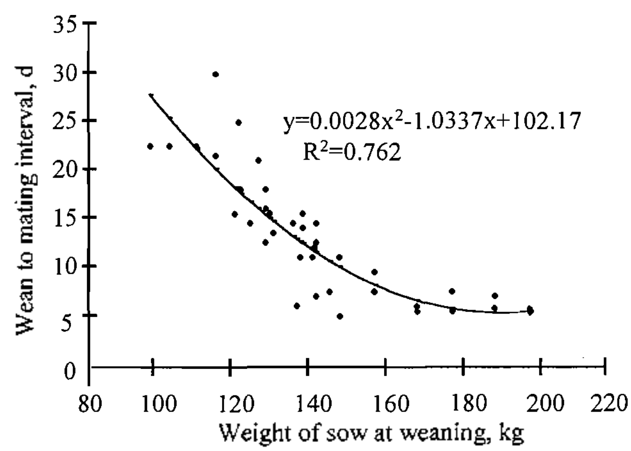

Figure 3. Impact of sow wean weight and wean to mating interval for first litter sows (Williams and Mullan, 1989). The data was derived from 6 studies and suggests that a wean weight of approximately 150 kg was needed to minimize wean to mating interval when nursing relatively large litters. This can be accomplished by feeding to promote net body gain during pregnancy and then to maximize feed intake during lactation. Nutrient levels should minimize body protein and bone mineral loss.

severe to reduce embryo survival (Pond et al., 1968; Aherne and Williams, 1992). Excessive feed intake adversely affects embryo survival (Hughes, 1993). Dyck and co-workers (1980) reported that increased feed level post-mating (from 1.5 to 3.0 kg/d) was associated with a decrease in plasma progesterone and a reduction in embryo survival (82.8 vs 71.9%) in sows. This agrees with recent reports by Ashworth (1991) and Jindal and co-workers (1996) with gilts. The latter fed from 1.9 to 2.5 kg/d at first mating to 15 d pregnant. They observed a reduction in embryo survival at 15 d (86% vs 67%) and fewer viable embryos at 25 d (9.8 vs 12.3) post-mating when compared to 1.8 kg/d. A high feed level during the first 24 to 48 h after mating appears to be especially detrimental to litter size.

Increased embryonic loss is consistently associated with lower progesterone in the early stages of pregnancy (Hughes and Pearce, 1989; Foxcroft et al., 1996). Progesterone is important to uterine quiescence and in preparing the uterus for embryo implantation. Low feed level results in increased plasma progesterone, which mediates an increase in embryo survival (Jindal et al., 1996). The emaciated weaned sow may represent an exception since a high plane of feeding in early pregnancy appears to be beneficial. In an experiment at the University of Alberta (cited in Aherne and Williams, 1992), sows were fed either 6 kg or 3 kg/d during lactation. From 48 h after mating, sows from each group received either 3.6 kg or 1.8 kg/d until d 25 of pregnancy. Pregnancy feed level did not influence number of embryos or embryo survival rate to 25 d for sows receiving 6 kg/d during lactation (avg. 14.1, 82.6%). Sows with extensive weight loss (fed 3 kg/d) during lactation had a higher rate of embryo mortality but number of embryos surviving and percent survival were improved by the higher (3.6 kg/d) feed level during early pregnancy (75.8% vs 67.4%). The fewest embryos and greatest mortality were associated with a low plane of intake in lactation that was not corrected during early pregnancy (11.5, 67.4%).

A prudent practice may be to feed approximately 1.5 × maintenance to gilts (1.8 kg/d) and sows (2.2 kg/d) until about 72 h post-mating. Females that are extremely thin at weaning are expected to have high embryo mortality and will benefit from a higher plane of feeding (3.5 kg/d). Sow feed intake 72 h after mating should be determined by body condition.

Mid-pregnancy nutrition

The nutritional strategy for the remainder of pregnancy should be to achieve moderate growth and to reclaim body reserves that were lost during the previous lactation. An allowance of 30 to 35 kg net body gain is important to first and second litter sows. A P_2 fat thickness of 17-20 mm at farrow is a prudent endpoint. Williams and Mullan (1989) suggested a wean weight minimum of 150 kg to minimize wean to mating interval (figure 3). This illustrates that a minimum pool-size for body protein and fat is needed to support rapid return to estrus. The insult of large body protein and fat losses to support lactation is proportionally greatest for young sows and compromises the optimum metabolic state for reproduction.

Maternal nutrition at key times may affect fetal development and consequently postnatal growth (Greenwood et al., 2000). It is not possible to increase pig birth weight by a high plane of maternal nutrition until after 80 d pregnant (Noblet et al., 1985) but improvements are modest and variable (Aherne and Williams, 1992). Plane of nutrition between 20-80 d pregnant may be important to muscle fiber number or myonuclei in piglets at birth and thereby potential postnatal growth. There is considerable public debate about whether doubling sow feed intake at a critical point in pregnancy will enhance muscle fiber number and benefit postnatal growth. Dwyer and co-workers (1994) reported that this tends to improve secondary muscle fiber number at birth and growth and efficiency of gain from 25-80 kg. This is at best preliminary since relatively few pregnant sows were used.

Fetal myogenesis: Muscle fiber number is positively correlated with growth and efficiency potential (Dwyer et al., 1994). Muscle fibers develop prenatally in 2 stages. Primary muscle fibers form between d 20-50 of pregnancy and are believed to be genetically fixed. Secondary muscle fibers form on the surface of primary fibers between 50-80 d. Secondary fibers are susceptible to environmental factors in utero. Muscle fiber number appears to be fixed by birth. Severe feed restriction of pregnant sows reduces postnatal growth (Pond et al., 1985; Pond and Mersmann, 1988). Maternal under-nutrition in pregnant rats also reduced postnatal growth (Wilson et al., 1988). This work seems impractical but emaciated or extremely thin sows may yield a similar result.

Jagger (1997) was not able to reproduce the benefit reported by Dwyer and co-workers (1994). His group conducted a trial where multiparous sow feed intake was doubled between d 25-80 of pregnancy. Sows were fed once daily and progeny growth evaluated from 30 to 90 kg. Since growth rate and feed conversion were not improved, they concluded that muscle fiber number or myonuclei was probably not increased (table 2). This is consistent with a more detailed test of prenatal nutrition on muscle chemistry and post-natal growth in sheep (Greenwood, 1997). Alternatively, somatotropin injection of pregnant sows during the critical period has proven to increase fetal muscle fiber number (Rehfeldt et al., 1993).

Maternal growth: The feed requirement for pregnant sows can vary by 30-50% within a herd depending on the attention given to body reserves. In practice, the main determinants of the energy requirement are body condition and phase of pregnancy (first 72 h after mating and late pregnancy) and not body size. This is illustrated in table 3. The NRC Sow model (1998) was used to generate energy and lysine needs for 7 parities during mid-pregnancy. Net maternal gain reflects reasonable expectations for tissue growth and yields the minimum expected weight after 6 litters. Feed levels allow for moderate weight gain and assume that body condition is near optimum and that temperature is thermal-neutral. Maintenance represents about 75 to 85% of the total energy requirement in younger and older sows respectively (Noblet et al., 1990).

The objective with young females should be to increase body protein and fat mass without making them fat. The amount to be fed to first and second parity sows is relatively similar to older, heavier sows since net maternal gain evolves from planned to obligatory gain with advancing age. A P_2 fat depth at farrowing of 17-18 mm is a realistic endpoint (assumes 1 mm fat loss=2 kg fat). The daily requirement for feed would need to be increased by about 60 g for each 1℃ below the critical temperature for cold. This is approximately 18℃ for sows in dry stalls and 14℃ in group pens. This requirement would be higher for thin sows since their maintenance requirement is higher.

Pregnancy feed level normally includes recovery of body reserves for 30-45 d. Absolute minimums for maintenance, late pregnancy and for body fat recovery are shown in table 4. A reasonable endpoint for body condition is 2.5 to 3.0, which we equate to 16-18 mm P_2. Feeding strategies require ultrasonic validation on a herd basis. Fat depth is symbolic of energy input in relation to energy expenditure and the need for adipose recovery.

Mammary Development: Mid-pregnancy is also a preparatory period for mammary tissue. The female's capacity for milk synthesis depends on the number of secretory cells and the critical period for cell proliferation is between d 75 to 90. Cell differentiation occurs between d 90 and parturition, which gives cells the biochemical ability for milk synthesis (Kensinger et al., 1982). There is evidence that excess energy and body fatness is detrimental to cell number and subsequent milk yield in gilts. Weldon and co-workers (1991) attempted to stimulate mammary cell proliferation in gilts by altering nutrition in the last third of pregnancy (after d 75). An increase in energy to 10.5 Mcal/d (vs 5.7) reduced cell number, which is expected to impair the capacity for milk synthesis during lactation. Head et al. (1991) modified body composition in gilts prior to breeding and observed that fat and lean females differed in the number of milk secretory cells at parturition. Fat gilts had fewer cells, based on DNA content, and produced less milk (7.0 vs 9.0 Liters/d) during lactation.

Late pregnancy nutrition

Nutrient needs increase exponentially in late pregnancy. An increase in feed level during this phase will prevent loss of maternal body protein and fat that would otherwise be mobilized to support fetal and mammary growth. Sows will lose substantial amounts of body fat if energy intake is not sufficient. Sows fed at about maintenance (6.0 Mcal DE/d, 182 kg

Table 2. High feed intake at a strategic point in pregnancy (d 25-80) does not increase postnatal growth rate in progeny[a]

Item	Feed level: Standard	Feed level: High	SEM
No. sows	7	7	-
No. pigs tested	32	32	-
Progeny growth			
Gain, g/d	875	875	14
Feed/gain	2.23	2.21	0.03
P_2 fat, mm	10.6	10.4	0.5
Lean %	57.2	56.8	0.6

[a] Courtesy of S. Jagger (1997, Dalgety Agriculture and PIC USA). Sows fed twice daily at 2.6 or 5.2 kg/d. Progeny growth assay from 34-96 kg with pens of 8 each. No statistical differences were observed.

Table 3. Predicted dietary energy and lysine needs to support different rates of growth during pregnancy over the life-cyle[a]

Litter no.	Body weight at mating (kg)	Net pregnancy gain (kg)	Diet intake (kg/d)	Predicted NRC ME (kcal/d)	Total lysine (g/d)
First	125	35	2.15	6,930	12.3
2	150	35	2.25	7,250	12.5
3	175	25	2.25	7,250	12.3
4	190	20	2.25	7,250	11.9
5	200	15	2.20	7,090	11.5
6	210	13	2.20	7,090	11.4
7	218	11	2.20	7,090	11.1

[a] Computed using the 1998 NRC Gestation Model. Assumed 3225 Kcal NRC ME/kg diet and 12 fetuses (litters 1-2) or 14 fetuses (litters 3-7). Total lysine levels shown using assuming a Corn-Soya diet. True ileal digestible amounts estimated by 0.83×total lysine. Energy and feed amounts assume that no body reserves need to be recovered. Adjustments for body reserves are shown in table 4.

BW) were shown to be in negative energy balance in late pregnancy (Noblet et al., 1990). At least 7.3 Mcal DE/d is needed to prevent this. We calculate that about 2.5 kg body fat would be mobilized if fed 6 Mcal/d from d 90. Cole (1990) estimated that up to 9.5 Mcal DE/d was needed from d 90 to parturition to maintain P_2 fat depth in sows.

Protein needs increase during late pregnancy. Nitrogen retention is estimated to increase from 9-10 g/d at mid-pregnancy to 17-18 g/d in late pregnancy (Noblet et al., 1985; Dourmad et al., 1996). Protein deposition rate increases 2-fold in the conceptus and 3-fold in mammary from d 100 to farrow (Whittemore, 1993). Milk secretory cell proliferation appears not to benefit from increased diet protein (Weldon et al., 1991; Kusina et al., 1995). However, protein restriction of gilts during pregnancy (16 vs 8 g/d) led to reduced piglet growth rate (figure 4). This difference may be related to the amount of 'labile' protein reserves that are available for mobilization during lactation since secretory cell number appeared not to be altered (Kusina et al., 1994, 1995).

Progressive increases in feed intake during late pregnancy resulted in modest and variable increases in pig birth weight (Aherne and Kirkwood, 1985). Piglets from very thin females might benefit more from relatively high feed levels than piglets from sows in adequate body condition. Excessive maternal gain and fatness can predispose the sow to dystocia at farrowing and decreased sow longevity (Dourmad et al., 1994). Insufficient recovery of body reserves may compromise the sow's ability to produce milk because of low body reserves. Thin sows are unable to mobilize adequate body reserves to support milk synthesis if restrictively fed. A realistic endpoint for body fatness is 16-18 mm P_2 fat. There is no advantage for more than 22-24 mm P_2 and sows having <12 mm P_2 at farrow are probably in a compromised position.

A phase feeding strategy during pregnancy is advised (vs Constant feed level throughout). It involves feeding the required amount of diet for each stage. While total amount fed may be more important than pattern of feed, phase feeding accommodates (1) early pregnancy embryo viability (0-72 h minimum), (2) growth and recovery of body reserves (to 90 d pregnant) and (3) exponential fetal and mammary growth (d 90 to 2 d prefarrow). Conservation of body protein is important to litter size in young sows and for mammary development in general.

Table 4. Body reserves management in pregnant sows: Minimum feed needs to reclaim body reserves and to support pregnancy for a 182 kg sow

Body condition score	Average P_2 fat depth, mm	Minimu intake, kg/d
1	8 to 10	3.5[a]
2	12 to 14	2.8[a]
3	16 to 18	2.2
Maintenance		1.6
Maintenance+Growth (20 kg)		2.2
Maintenance+Conceptus+Mammary +Growth		2.8[b]

[a] Computed using the 1998 NRC Gestation Model. Assumed that 2.0 kg of fat deposition=1 mm fat depth and that the gestation diet has 3,225 kcal NRC ME/kg. Amount to reclaim reserves to a condition score=3 if fed for 60 days of pregnancy.

[b] Assumes modest rat maternal growth from line above as Conceptus+Mammary growth now becomes the priority.

FEEDING THE LACTATING SOW

The feeding strategy during lactation should be to maximize feed consumption. Nutrient specification is critical but secondary. Feeder type and feeding method are too often inadequate for prolific sows. It is normal for lactating females to lose weight (<10 kg in 21 d) but excessive loss may result in prolonged WEI and decreased litter size. These may occur with low feed consumption or they can occur with either low energy or low protein intake (van der Peet-Schwering et al., 1998). The importance of lactation feed intake on subsequent reproductive output increases with the number of pigs nursed and with younger sows as compared to older sows.

Prolific females are driven to high milk production by their large litters. However, voluntary intake in first litter females tends to be lower than needed to insure adequate intake of nutrients when they are fed a herd lactation diet. Deficits for energy and amino acids (and calcium, phosphorus) can lead to extensive tissue catabolism. Aherne (1994) concluded that a 20% deficit in feed intake of first litter females (5.5 to 4.5 kg/d) resulted in a second litter size decrease of approximately 1 pig (5-study review). For multiparous females, the nutrient needs for milk production are more nearly met by increased feed intake or by a larger body size to derive nutrients from. However, they sometimes suffer from a progressive decrease in body reserves because we underestimate the amount of feed that it takes to rebuild them during the ensuing pregnancy.

Vesseur et al. (1994a) illustrated the importance of body size in their attempt to relate weight loss during lactation to WEI. First litter females that lost more than 7.5% of their post-farrow weight exhibited a prolonged WEI (2 to 4.7 d). The effect was less pronounced in second litter sows but WEI was not influenced by weight loss in third and fourth litter females. The concern for a prolonged WEI involves more than the increase in non-productive days for the sow. They observed that sows inseminated 5 d after weaning had a higher farrow rate and more piglets than sows inseminated between d 9 and 12 post-wean (Vesseur et al., 1994b).

Nutritional burden of lactation

The nutritional burden imposed by nursing a large litter was illustrated using prolific first litter females (Boyd and Touchette, 1998). Sows weaned 10.2 pigs of 11 pigs placed per litter and nursed up to 21 d. A practical diet (0.95% total lysine) was fed with slight restriction for the first 5 d of lactation and then full-fed thereafter. Litter growth rate was determined at 5 d intervals to estimate milk output. This allowed us to calculate energy and amino acid balance at different points in lactation (table 5). Classic relationships were used to predict the extent of body protein and fat mobilization so that diet and feeding strategy could be studied and amendments proposed (as described by Whittemore and Morgan, 1990 and applied by NRC 1988).

Milk output averaged nearly 10 kg/d for the 21 d lactation (assuming 4 g milk/1 g piglet gain). Almost 8 kg/d was produced during the initial 5 d (d 1-6). Energy balance was negative throughout but especially during d 1-6 when a conservative feed strategy was used. An estimated 10.4 kg of body fat would be mobilized to meet milk energy needs for an 18 d lactation (@ 0.58 kg/d). This would decrease to 8.5 kg if 9.2 pigs were nursed which is an 18% decrease. Approximately 0.65 kg/d of feed would be needed for 60 d (d 5-65) to reclaim the extensive mobilization of body fat stores (10.4 kg).

Lysine needs were also predicted (table 5). Calculations suggest that an average lysine intake of 69 g/d was needed to support milk production (9.84 kg/d) and maintenance with no mobilization of body protein. This is in close agreement with the relationship developed by Pettigrew (1993, figure 4) of 26 g lysine/kg litter growth/d plus a maintenance requirement of 49 mg lysine/kg$^{0.75}$ body weight (2.55 g/d). This calculation yields 66 g lysine/d but assumes that an additional 6.7 g lysine/d is derived from body protein mobilization (98.7 g protein/d).

Lysine for milk synthesis=0.026 (Litter growth rate, g/d) - 6.71.

The significant lysine and energy deficit suggests that feeding strategy and lysine level were inadequate. The conservative feeding during d 1-6 is sometimes recommended but resulted in an extreme negative balance of energy and protein. Catabolism of uterine protein occurs during early lactation and may partially offset the extensive d 1-6 deficit. However, 45% of the estimated total loss in body protein during the 21 d lactation (5.1 kg) was lost during the first 6 d. This insult to body protein for the entire lactation is estimated to be 17.5%.

Suboptimal feed intake at any point during lactation can have a negative influence on subsequent reproductive performance in sows (Koketsu et al., 1996; Tokach et al., 1992b). Therefore, it is important

Table 5. Predicted energy and lysine needs for prolific first litter sows[a,b]

	Lactation interval, days				
Item	1-6	7-11	12-16	17-21	Mean
Litter growth, kg/d	1.95	2.54	2.70	2.63	2.46
Milk output, kg/d	7.80	10.16	10.80	10.52	9.84
Feed intake, kg/d	3.21	5.74	6.77	7.59	5.83
Energy balance, Mcal ME/d					
Required	20.43	24.96	26.19	25.65	24.30
Deficit	-9.59	-5.56	-3.31	0	-4.61
Fat mobilized, kg/d	-1.20	-0.70	-0.42	0	-0.58
Lysine balance, g/d					
Required	55.9	71.5	75.8	73.9	69.3
Deficit	-25.4	-17.0	-11.5	-1.8	-13.9
Protein mobilized, g/d	-467	-313	-211	-33	-256
Cumulative protein mobilized, kg	2.33	3.89	4.95	5.12	-
Dietary Lysine, %[c]	1.57	1.12	1.01	0.88	-

[a] Adapted from by Boyd and Touchette, 1998.

[b] Assumptions: 30 females, 195 kg bw; fed conservatively 5 days then full fed at 4 times/day; 10.2 pigs weaned/litter; 4 g milk per g piglet growth; maintenance=$W^{0.75} \times 105.6$ Mcal; 1.0 kg milk requires 1.92 Mcal ME; 3.38 Mcal ME/kg diet; body fat energy to milk 85% efficient and 9.39 Mcal/kg fat. Maintenance lysine=49 mg/kg$^{0.75}$; Milk=5.7% protein which is 7.0% lysine; lysine digestion=86% and absorbed lysine used at 70% efficiency; mobilized protein=6.8% lysine.

[c] Dietary lysine need assumes 90% of lysine balance.

to optimize feed intake of lactating sows during each week of lactation. Sows display diverse feed intake patterns during lactation for reasons that are not entirely clear (Williams, 1998; van der Peet-Schwering et al., 1998). Table 5 shows the merit of feeding to accommodate a rapid increase after farrowing. Sows that have a gradual increase throughout lactation can achieve a similar average intake with no apparent difference in reproduction (Koketsu et al., 1996).

Concept of an optimum body protein mass

Table 5 illustrates how the factorial approach can be used to make dynamic estimates of the impact of lactation length and feeding strategy on body fat and protein reserves. We estimate that about 5.0 kg of body protein would be mobilized in an 18 d lactation period (18 d×256 g protein/d) and that only 400 g could come from obligatory uterine catabolism (Dr. Hans Stein, personal communication). Assuming sow weight is 15% protein, then these females had 29 kg of total body protein (15%×195 kg) and mobilized a net 15.9% of total protein mass. We propose that this should not exceed 10-11% in first litter females (3.22 kg or 179 g/d) in order to realize a 1 pig increase in second litter size response (Touchette et al., 1998a). A higher proportion body protein mobilization is allowable for older females because of their increased body size and body protein pool.

Everts (1994) estimated that a biological drive to attain a target body protein mass exists and that it is at least 35 kg for the sow. This would be reached by fourth parity assuming that a 150 kg gilt has 22-23 kg of body protein and gained 3-5 kg protein/parity. The limit to protein reserves loss was estimated to be about 25% of total body protein in the lactating dairy cow (Botts et al., 1979) and rat (Pine et al., 1994). However, this may be unrealistic for younger litter-bearing females when subsequent reproduction is considered (vs milk output). This would be far too harsh for the first litter sow in view of the evidence presented earlier for litter-size.

The advantage for a large body mass when protein mobilization is extensive is illustrated in table 6. We computed body protein mass for young sows that entered the breeding herd at different body weights (165 vs 195 kg post-farrow weight) and for older females (225 kg). A 4 kg loss in body protein represented 16.6% of the total pool for 165 kg females but only 12.1% for older females.

Table 6. Estimated whole-body protein mass and proportion of body protein mobilized in support of lactation for sows of different age and body size

	Parity×post-farrow body weight, kg		
Item	P-1, 165	P-1, 195	P-3, 225
Total protein mass, kg[a]	24.7	29.3	33.8
Protein loss, kg[a]	4.1	4.1	4.1
Protein loss, %	16.6	14.0	12.1

[a] Theoretical estimates of whole-body protein mass assuming 15% protein content of body weight.

[b] Theoretical estimate of body protein loss assuming 17-18 d lactation for P-1 sows presented in table 5 (at 195 kg bw). P-3 data taken from counterparts to P-1 sows represented in table 5.

Lysine response curve - classic but misleading

Our perspective on amino acid nutrition for prolific lactating sows is changing because of recent research. Lysine has been studied most extensively because of its first limiting status in practical diets. Pettigrew (1993) brought some common sense to the extraordinary variation in reported lysine needs by regressing maximum litter growth rate on optimum lysine level from published studies. This approach yielded the classic linear response curve. We updated this data set with the revised equation being nearly identical to that originally reported by Pettigrew (figure 4).

We have long known that the lysine requirement for lactation depends on the criterion selected (Lewis and Speer, 1975). The classic linear response for litter growth rate is misleading in view of the newly

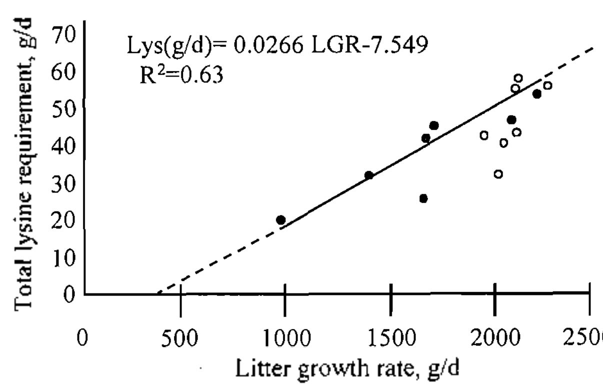

Figure 4. The dietary lysine requirement increases in a linear manner with litter growth rate (LGR). Pettigrew (1993) was the first to derive the response curve using data published during 1972 to 1991 (solid circles). The curve was updated, using data published between 1993 and 1997 (open circles). The new equation is remarkably similar to the original: Total dietary Lysine need (g/d)=0.026(LGR, g/d)-8.38. The line slope indicates that 26 g Lysine is needed per day for each 1 kg of litter growth. The negative intercept (8.38) is an estimate of the amount of body lysine mobilized, which equates to 123 g body protein per day (assuming protein=6.8% lysine). This is 2.46 kg of body protein for a 20 day lactation.

discovered effect on litter-size in first litter females. The response between lysine input and litter growth rate is also difficult to show with short lactation periods (e.g., 14-19 d), provided that the female has adequate body protein reserves to mobilize. King and co-workers (1993) illustrated that the lysine requirement to minimize body protein loss is higher than required for milk production; the lysine level that minimizes protein loss will minimize WEI and subsequent litter size in first litter females. The ability to influence litter size by amino acid nutrition is a new dimension in our understanding.

Amino acid and litter size - new dimension

Touchette and co-workers (1998a) provided a powerful illustration of these concepts by titrating the lysine requirement for first litter females under commercial conditions. They observed that the lysine need for minimum weight and loin area loss (50-54 g/d) in a 17 d lactation was much higher than was needed to maximize litter growth rate (32 g/d). This suggests that young prolific females were able to mobilize enough body protein (14% change in loin area) to support lactation but formulating to minimize body protein loss resulted in an increase in second litter size by 1.2 pigs per litter.

Length of lactation was also important when determining lysine need since the difference in response to graded lysine levels was not statistically significant until 17 d (vs 14 d). It is still unclear whether conseruing body protein is important for improving litter size of second litter sows, but the fact that the latter tend to have a larger body protein mass makes this less likely.

Another potentially important observation emerged from the study by Touchette et al. (1998a). Their results suggest that form in which amino acids are provided may be either positive or deleterious to future litter-size. This needs to be verified, however, it illustrates why next litter-size must be included as a criterion in amino acid and energy studies during lactation. Four diets were formulated to provide 0.67, 0.86, 1.06 or 1.25% of apparently digestible lysine. Lysine level was elevated by intact protein but synthetic methionine, valine and threonine were used to maintain equivalent ratios to lysine as provided by the 0.67% control. A fifth diet was identical to the 1.06% counterpart except that all synthetic amino acids were removed. Ratios to lysine were adequate for diet 5 based on the new NRC (1998) and level of litter growth.

Increasing dietary lysine intake while maintaining constant amino acid ratios to lysine for valine, threonine, and total sulfur amino acids (diets 1-4) resulted in a linear ($p<0.05$) decrease in the percent loin area but second litter total born also declined (-0.5 to -1.4 pig/litter). Deletion of synthetic amino acids from diet 5 (1.06%) resulted in an increase in total born (12.9 vs 11.2, $p<0.05$) when compared to its counterpart and to the 0.67% control (12.9 vs 11.7, $p=0.13$). Diet energy density (ME) and daily energy intake were similar for the 1.06% apparently digestible lysine counterparts. The detrimental effect of extensive synthetic amino acid addition (other than lysine) is possibly due to the amount of methionine required to equal that provided by intact sources for the control (0.67 methionine+cystine : 1.0 Lysine). This is in considerable excess of the NRC (1998; 0.49 : 1.0).

The practical benefit of this information is that lifetime pig output could be reduced by more than 1 pig by first litter nutrition. As new technologies (e.g., genetic markers for litter-size) improve our ability to select for improved litter size, nutrition will become increasingly important as a constraint to genetic expression.

Energy dependence of the lysine requirement

Both energy and amino acid intake are important to lactation and subsequent reproduction. Glucose is the most important nutrient to milk production and represents about 60% of the total mass taken up by the mammary gland. Almost 70% of total body glucose is used by the mammary gland (Boyd and Kensinger, 1998). Milk synthesis in lactating dairy cows is directly related to glucose availability and this is dependant on feed intake.

This energy-dependence of milk synthesis in sows was illustrated by Tokach and co-workers (1992a). They observed that the ability to take advantage of lysine for milk output was dependent on the level of feed intake. As energy intake increased, the response to lysine intake increased. However, this relationship is probably less strict than we have observed with growing pigs. We expect that the ability to produce milk in the absence of adequate energy intake depends on the amount of body fat that is available for mobilization. This concept is consistent with research by Sauber (1994). Thus, the lysine requirement for lactating sows is influenced by energy intake and by the amount of mobilizable body fat.

Requirement for other amino acids

Adequate levels of other amino acids must also be provided and could be estimated if the ideal pattern relative to lysine is known. The pattern proposed by the NRC (1998) was derived from empirical studies and by sophisticated work involving mammary amino acid uptake relative to output (Trottier et al., 1997). The latter can be a helpful tool since >90% of the protein requirement during lactation is due to mammary uptake (Boyd and Kensinger, 1998). A pattern that is based on the amino acid composition of milk can be misleading for reasons that were discussed earlier (Boyd and Kensinger, 1998).

The problem is that the ideal pattern among amino acids for lactation is not known with enough confidence. We are not able to predict the second limiting amino acid or its required level and this must be known if the correct amount of synthetic lysine is to be determined. This part of the review is limited to (1) a discussion of the validity of the proposed NRC pattern (1998); and (2) the consequence of extensive synthetic lysine intake when lactating sows are in negative protein balance.

Proposed ideal amino acid pattern

The proposed pattern for essential amino acids by the U.S. NRC (1998) is presented in table 7. The minimum amount of each that must be provided preformed by the diet is expressed as a proportion to lysine. More of an amino acid may be required to support mammary growth and milk synthesis, but the NRC pattern reflects only that amount which is required in the diet beyond endogenous synthesis. For example, the required amount of arginine can be completely synthesized during pregnancy so it is not an essential amino acid. During lactation, it is essential since only 50-60% is synthesized. The NRC requirement for arginine reflects only that portion that the body is not able to synthesize.

The pattern of amino acid uptake by mammary glands is also shown in table 7. The g/d uptake for each amino acid is expressed relative to the g/d uptake for lysine. Mammary uptake reflects the amount of each amino acid that is taken up for milk synthesis and mammary growth. This information can be helpful in estimating the need for certain amino acids but it has limitations which could result in an over-estimate of the dietary need for some (e.g., arginine). Empirical verification will still be an important tool in validating proposed patterns.

The dietary pattern for a lactation diet formulated to 1.05% lysine (0.914 true ileal digestible lysine) is shown in table 7. This is realistic for a prolific sow having a litter growth rate of 2.50 kg/d and consuming a minimum of 5.5 kg feed/d. For this diet, valine appears to be second limiting based on the NRC pattern. Threonine is adequate but appears to be third limiting. The mammary pattern supports this view but the milk pattern places threonine as second limiting. This illustrates the problem of not knowing with certainty the second limiting amino acid. The tryptophan : lysine ratio for mammary tissue is probably incorrect given the low concentration and the difficulty of doing physiological and chemical measures.

Formulating to 1.05% lysine changes the dietary margin for valine, isoleucine and leucine when compared to a 0.65% lysine diet (typical 15-20 years ago). It is unclear whether the relative amount of isoleucine, leucine and valine uptake is obligatory and whether an apparent deficiency of one might be compensated for by increased mammary extraction (or increased use) of another branch-chain amino acid.

The NRC (1998) pattern for prolific females is a reasonable estimate given available information. Threonine and valine were adjusted downward relative to lysine (0.72 to 0.62; 1.00 to 0.86 respectively) from their prior recommendation.

Consequence of extensive synthetic lysine use

The second point is that extensive synthetic lysine use may compromise lactation performance unless sows are in positive nitrogen balance. Touchette and co-workers (1998b) supplemented diets formulated to 0.94% total lysine with 0.0, 0.075, 0.150 or 0.225% of synthetic lysine. Diets were fed *ad libitum* to lactating sows (parities 1-3). All sows lost body protein and were, therefore, in negative nitrogen balance. The 0.075% synthetic lysine diet did not affect litter growth rate but higher levels caused a linear decline with practical consequences on wean weight and litter-size weaned. A fifth diet contained 0.150% synthetic lysine and synthetic methionine,

Table 7. Proposed pattern of essential amino acids (NRC, 1998) for lactating sows compared to the pattern of uptake by the mammary glands (arterio (-) venous) and that provided by diets formulated to different lysine levels

Amino acid	Milk[d]	Mammary[a] A-V	'98 NRC	Diet, %[b,c] 0.65	1.05
Lysine	100	100	100	100	100
Leucine	115	156	113	221	171
Valine	73	90	86	97	83
Arginine	66	133	58	123	122
Isoleucine	55	79	56	79	74
Threonine	58	68	62	75	67
Phenylalanine	56	66	54	84	73
Histidine	40	32	40	59	49
Methionine	23	28	26	39	31
Tryptophan	18	36	19	21	22

[a] Lysine set=100. Each amino acid taken up per day set as a ratio for lysine.

[b] Diets formulated to total lysine level using corn, soybean meal (48% protein) and lysine HCl (0.075% of diet). Ratio of each amino acid to lysine involved true ileal digestible values for amino acids (NRC 1998).

[c] 0.65% lysine provides 34 g lysine/d at 5.30 kg feed/d and supports 1,300 g litter growth/day. 1.05% lysine provides 59 g lysine/d at 5.6 kg feed/d and supports 2,500 g litter growth/d.

[d] Milk pattern taken from R. H. King as published in 'The Lactating Sow' (Chapter 7).

threonine and tryptophan to restore ratios to lysine that were equivalent to the control. This failed to correct the negative response to extensive synthetic lysine use and suggests that one or more other amino acids were limiting. The valine : lysine ratio was slightly below the mammary and NRC patterns (0.85 vs 0.90, 0.86). This is also true for isoleucine in regard to the mammary only. The leucine : lysine ratio was well above by any standard (milk, NRC, mammary).

Is valine limiting in practical diets?

Litter growth rate was reported to be improved and body weight loss less when lactating sows were fed diets having a valine to lysine ratio as high as 1.20:1.0 (Richert et al., 1997; Moser et al., 2000). This is greater than provided by practical diets (formulated to meet lysine needs) and it is greater than expected based on relative mammary uptake. We used the data reported by Trottier et al. (1997) to compute the maximum valine to lysine ratio. It should not exceed 0.90:1.0 unless valine compensates for an isoleucine deficit (Boyd and Kensinger, 1998). Valine is glucogenic but this role seems quantitatively doubtful except under extreme feed intake restriction. A role in conversion to so-called non-essential amino acids may be more likely.

We investigated the value of adding synthetic L-valine to a practical corn-soy diet for lactating sows (n = 179) above levels prescribed by the NRC (1998). Three diets were formulated to contain 0.90% total lysine with the control having a valine to lysine ratio of 0.90:1.0 (similar to mammary uptake). Synthetic valine was added to create test diets with ratios of 1.05 and 1.20 to 1 part lysine. This study failed to show an advantage in formulating practical corn-soy diets to a valine:lysine ratio greater than 0.90 to 1.0, which gives credibility to the NRC estimate (Boyd et al., 1999; table 8).

Extraordinary nutrient needs of the elite lactating sow

Comparison of the elite modern sow (13.6 kg milk/d) to a standard of the past (7.5 kg/d) illustrates how dramatic the change has been in glucose and amino acid needs to support milk synthesis (table 9). Second and third litter counterparts (n=65) to those presented in table 5 averaged 10.9 kg milk output/d based on litter weight gain. The 10 most productive sows produced an average of 13.6 kg milk/d. This is almost twice that of the past (7.5 kg/d) and it was 25% greater than the average for this study. Sows that produce more milk require more feed so feeding management becomes increasingly important. The elite sows are more likely to be the thin sows in modern production.

Glucose represents about 60% of the absorbed substrate mass by the mammary (Boyd and Kensinger, 1998). The elite sow is expected to absorb 1.96 kg/d, which amounts to 76% of the whole body requirement (table 9). The reference sow is expected to use 1.06 kg glucose/d (63%) to support mammary growth and milk synthesis. Glucose availability is probably the first limit to milk synthesis and is a direct function of feed intake (Annison, 1983). Milk fat output for the elite sow (973 g/d) is extraordinary and poses an unnecessarily high energetic cost. Mobilization from adipose and mammary use of glucose for fat synthesis is greater than required for optimum growth under commercial conditions (see Boyd and Kensinger, 1998). Methods to suppress mammary fat synthesis may benefit the saw and enhance piglet growth because the lysine:energy relationship in sow milk is

Table 8. Valine to lysine ratio in practical diets for lactating sows: performance for litters 1 through 4

Item	Valine:lysine ratio					Overall
	Unit	0.90	1.05	1.20	SEM	
No. Sows		59	60	60	-	179
Lactation length	d	19.2	19.5	19.4	0.3	19.3
Sow wt change	kg	-10.0	-10.1	-9.3	1.5	-9.2
Feed intake (7.5% loss)	kg/d	7.02	7.04	7.05	0.07	7.02
Loin depth change	mm	-1.9	-1.8	-2.2	0.5	-1.9
Backfat change	mm	-2.3	-1.6	-1.7	0.3	-1.8
No. pigs start	p/L	10.9	10.7	10.9	0 2	10.9
No. pigs weaned	p/L	10.2	10.0	10.2	0.2	10.2
Litter wean wt	kg	60.0	58.3	59.7	1.6	59.2
Litter growth rate	g/d	2245	2162	2233	71.5	2201
Dietary Lysine intake[b]	g/d	62.1	62.2	62.3	1.0	62.1
Calculated Lysine need[b]	g/d	64.0	61.8	63.8	2.0	62.9

[a] Valine linear and quadratic (NS, p>0.10).

[b] Predicted Lysine need is based on calculations used in table 5. Represents the amount needed to meet 100% of the requirement (assumes no obligatory mobilization of body protein).

not optimum for piglet.

The mammary gland dominates the amount and pattern of amino acids. Almost 95% of the daily lysine requirement would be needed for milk synthesis by the elite sow (table 9). The net lysine requirement for sows producing 13.6 kg milk/d is 58 g/d which amounts to about 97 g total lysine/d for a corn-soya diet. We do not expect the pattern of mammary amino acid uptake to be very different, but the pattern that is provided by the diet that is needed to meet the increase in lysine requirement would be.

Phase feeding of lactation diets

The sow herd is composed of two sow types with distinct differences in nutrient need: (1) First litter and thin sows and (2) multiparous sows in proper body condition. The former represents 50% or more of the herd and they require a higher percentage of dietary amino acids to minimize body protein loss during lactation. The first 10-12 d of lactation is the most demanding period. Percent lysine need was higher during early lactation than later in lactation (table 5). Aggressive full-feeding of a single diet during the first half of lactation could result in significant loss of body protein.

Table 9. Estimated needs for first limiting nutrients and milk nutrient output for the elite modern sow compared to a reference sow of the past

Item	Milk output kg/d[a]	
	7.5	13.6
Net energy, Mcal/d[b]		
Maintenance (NEm)	4.5	4.5
Milk (NEp)	11.8	21.9
Glucose, g/d[c]		
Maintenance	620	620
Mammary uptake	1,058	1,960
Net lysine, g/d[d]		
Maintenance	2.5	2.5
Milk	32.1	55.5
	Milk nutrient uptake	
	13.6 kg/d[e]	
Energy, Mcal GE/d	15.5	
Lactose, g/d	612	
Protein, g/d	762	
Fat, g/d	952	
Lysine:Mcal GE	3.68	

[a] Supports 3.48 kg/d litter growth (Boyd and Touchette, 1998).

[b] NEm=86.6 Mcal/d/$BW^{0.75}$. Assume NE=0.82 ME and that average body weight (bw) is 195 kg. NEp=1.92 Mcal ME/kg milk×0.82.

[c] Glucose use for maintenance=2.21 mg glucose/minute/kg BW. Glucose uptake=14.1 g/dL milk (Boyd and Kensinger, 1998).

[d] Maintenance lysine=49 mg/kg $BW^{0.75}$; Assumes milk is 5.7% protein, milk protein is 7.5% lysine and that 100% of mammary uptake is secreted in milk.

[e] Composition of milk assumed: Lactose, 4.5%; fat, 7.0%; protein 5.6% and assumed protein is 7.5% lysine. Energy density of milk, 1.14 Mcal gross energy/kg milk per.

Phase feeding of two diets should be utilized for prolific females during lactation. The lysine requirement for first litter and thin sows is (1) higher and (2) it may also be higher in early lactation as compared to later in lactation (depends on the rate of feed intake increase post-farrow; Koketsu et al., 1996). We propose a separate diet where possible and aggressive feeding early in lactation as a general practice for prolific females (approximately 10 pigs weaned/litter). In practice, implementation might involve either (1) a second diet or (2) hand addition of soybean meal to the normal lactation diet for the first 10-12 d for first litter and thin sows.

Phase feeding to accommodate environments with extreme heat (>30℃) is another consideration but it is not clear that diet can do much to prevent the extraordinary loss in sow weight, reduced litter growth rate and reproductive performance (Black et al., 1993; Prunier et al., 1996; Quinou and Noblet, 1996). We're not optimistic that diet can be manipulated enough to make a dramatic difference but formulations should involve low heat increment (high fat, low fiber) and a slight increase in dietary amino acid percentage to minimize body protein loss.

FEEDING FROM POST-WEANING TO MATING

Weaning is the time to assess the effectiveness of lactation feeding and to set objectives for recovery of body reserves. Limiting back fat loss to 2 mm and loin area change to about 10-11% from farrow to weaning (18-20 d) is evidence for good feeding management. Maintenance of body reserves begins with elevating feed level at about 90 d pregnant. Loss of body reserves also occurs postweaning.

Sows typically lose weight (8-10 kg) and backfat (1 mm) between wean and mating. This is probably due to (1) relatively low intake, (2) extensive loss of mammary weight and, (3) the energy required to eliminate nitrogen from catabolized mammary tissue. It is not clear what the feeding strategy should be to minimize the apparent loss in backfat and body weight during this period. Maximum intake seems logical but the level of protein is unclear since mammary protein is being mobilized in significant amounts and presumably useful to meet maintenance needs.

High post-weaning feed level has been reported to shorten the interval to service in first litter sows which results in a higher percentage exhibiting estrus within 10 d of weaning. It has no such effect on more mature sows that are in relatively good body condition (Aherne and Kirkwood, 1985). The response of first litter sows is variable and perhaps more dependent on body condition (Carroll et al., 1996 observed no effect). Absolute body weight at weaning may be the most important variable for young females (Mullan and Williams, 1989).

METABOLIC FUELS - REPRODUCTIVE LINK

A complete reproductive cycle is one of the most energetically expensive and challenging activities that a female can undertake. There is a growing body of literature in mammals that shows ultimate control of fertility by the metabolic state (Wade and Schneider, 1992; Wade et al., 1996). The animal integrates metabolic and endocrine signals and prioritizes long-term reproductive load accordingly. The mechanisms by which subsequent reproduction is affected by nutrition are not well understood but enough is known to understand how diet and feeding management interact to influence future reproduction. A review of mechanisms is beyond the scope of this paper. The reader is referred to a review by Williams (1998).

The neural mechanisms controlling pulsatile release of GnRH and consequently, LH secretion and ovarian function appear to respond to minute by minute changes in metabolic fuel availability. Fuel deprivation appears to inhibit LH secretion by acting on the hypothalamus to suppress GnRH secretion and on the pituitary gland to alter responsiveness to the releasing hormone. This occurs during lactation which has an important effect on the subsequent litter given the time required for ova maturation (Wade and Schneider, 1992).

Tokach and co-workers (1992b) showed that sows with prolonged WEI had fewer LH peaks and lower concentrations on d 14, 21 and 28 of lactation. Jones and Stahly (1995) reported a high correlation ($r= -0.55$) between mean LH in early lactation (d 5 or 10) with wean to mate interval. Thus, alterations in LH profile early in lactation are associated with subsequent reproduction.

Evidence for a link to nutrition was provided earlier by King and Martin (1989), who observed that sows restricted in protein intake during lactation have reduced LH concentration and have fewer LH pulses during lactation. Tokach et al. (1992) showed that energy and amino acid intake affect LH concentration in an interactive manner. At low energy intake, increasing lysine intake had little influence on mean LH. The influence of lysine intake increased as energy intake increased. Zak and co-workers (1997) used a creative strategy to show how the pattern of feed restriction was reflected in frequency and amplitude of LH pulses. These three studies show that mean LH is reduced by restriction of either amino acids or energy, that a lysine to energy interaction exists and that suckling and pattern of feed restriction affect LH secretion.

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