A ROLE FOR ENHANCED NUTRITION IN REPRODUCTION

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Summary

Nutrition can affect several components of reproductive efficiency such as the age at puberty, ovulation rate, embryo mortality, birth weight, and the duration of post-partum anoestrous. Many of the traditional strategies for managing farm livestock for reproduction have relied heavily on the use of the animal's own body reserves to buffer against dietary shortfalls. However increased demands for higher production mean that our current-day animals are often not given the same opportunity to build up body reserves as their counterparts of some years ago and this means that their reproductive processes are now more responsive to nutrition.

I. INTRODUCTION

Reproductive efficiency in domestic animals of agricultural importance is best measured as the amount of meat or milk produced per breeding unit per year. The two variables which influence efficiency the most are the age when animals commence to reproduce and the average number of reproductive cycles of each animal in the herd or flock. The biggest gains in efficiency are likely to be made by by providing an environment which encourages the females to begin breeding early in life and then managing them so they remain in the herd or flock reproducing at regular intervals. In non-seasonal breeders like the pig a delay of two months in the attainment of puberty might reduce efficiency only by 5 to 10 %. In seasonal breeders or animals grazing in seasonal environments the consequences of delays in puberty are often much greater because reproduction must be timed precisely so that the nutritionally-demanding events of late pregnancy and lactation occur when the diet is likely to be at its best. For these animals small delays in the attainment of puberty might mean that the first progeny are delayed for a whole year. Maintaining regular breeding intervals can also have a very large effect on reproductive efficiency. For example, efficiency will increase by between 40 and 50% if gilts can be managed successfully so that they remain in the herd and produce two rather than one litter. With each successive litter the gains in reproductive efficiency become progressively smaller but they are still significant. Similar gains apply in other species.

Nutrition directly influences several components of reproductive efficiency such as the age at puberty, ovulation rate and litter size, embryo mortality, growth of the fetus, birth weight and perinatal survival, lactation, and the duration of the post-partum anoestrous. In many commercial situations nutrition limits the growth of animals and hence is likely also to limit reproduction. Even intensively housed pigs given unrestricted access to food and not subjected to nearly the same fluctuations in nutrition as grazing sheep or cattle generally achieve growth rates of half to two thirds of their known potential. Thus improving the nutrition of animals in a wide range of production systems from intensively housed pigs to grazing ruminants is likely to enhance reproduction.

In this paper I will consider the important stages of reproduction and try to relate the way

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in which the diet affects these stages and those that follow. Limitations of space prevent this discussion from being all inclusive so I will use examples mainly from sheep and pigs because I am most familiar with these species. However since there are many similarities in the responses of animals to nutrition, many of the principles developed here with pigs and sheep should be applicable to other domestic animals.

II. PUBERTY

The earlier animals reach puberty and commence reproduction the greater are the potential gains in reproductive efficiency because the maternal overheads can be reduced. But entry into reproductive life commits the animal to an enormous expenditure of energy at a future date. In males the nutritional requirement for sperm production is very small but the energy expended in the pursuit of females and the defence of a harem can be large and it is not uncommon for males to lose substantial amounts of weight during the breeding season. For example, Soay sheep lose such large amounts of weight during the autumn rut that, unless they begin the rut with very good nutritional reserves, they will die the following winter. At the other extreme boars that are housed intensively in individual pens expend very little energy fighting other males, do not have to defend a harem and, consequently, need only a small amount of energy for sperm production, copulation and their own maintenance. In fact they may become lazy and reproductively unfit if overfed.

Puberty in the female is complex and seems to have a number of inbuilt safeguards to protect the animal from becoming pregnant too early in life until she is capable of bearing and rearing her young. Thus puberty is more a function of body weight or body reserves rather than chronological age and this has been well demonstrated in pigs by King (1989). He manipulated the growth of pigs as soon as they were weaned at three weeks of age by feeding them different amounts of a protein-adequate diet so that, by the time they were 170 days old, he had six groups of gilts ranging in weight from 60 to 118 kg. At 170 days he changed all gilts to a common feeding regime (2.2 times maintenance) and began to expose them to mature boars to induce puberty. He found a linear relationship between the proportion of gilts reaching puberty at 200 days and their live weight at 170 days of age (Fig. 1)

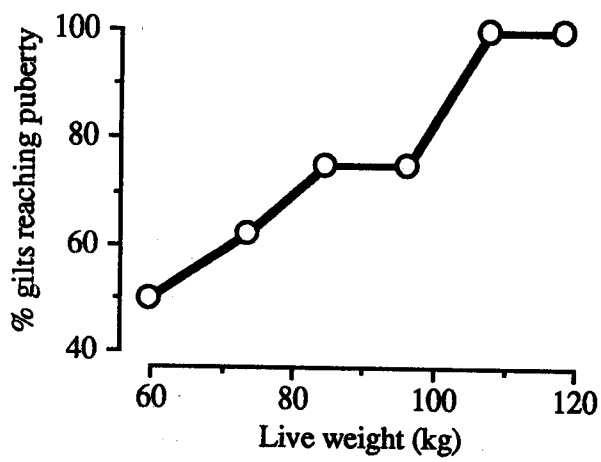

Fig. 1. Effect of live weight at 170 days of age on the proportion of gilts reaching puberty at 200 days of age

Not all studies show such a simple, elegant relationship between weight (or growth rate) and puberty. For example, from the reviews of den Hartog and van Kempen (1980) and

Paterson (1989) there is evidence for a positive, negative or zero relationship between growth rate and puberty depending on the data selected. In a recent large-scale experiment Young et al. (1990) found no relationship between growth rate and age at puberty of gilts. Beltranena et al. (1990) found a negative quadratic relationship between age at puberty and lifetime growth rate to puberty For pigs restricted in food intake and growing at less than 500 g/d from birth, an increase in growth rate reduced the age at puberty. For other gilts with growth rates of between 500 and 650 g/d there was no effect of growth rate on the age at puberty but, for gilts growing at more than 650 g/d, a further increase in growth rate retarded animals reaching puberty. The suggestion from this is that for very fast growing animals the hypothalamic-hypophysial-ovarian axis needs more time to mature while for slow-growing animals there is a need to reach a critical body weight.

Rather than body weight or growth rate per se as determinants of puberty, a more acceptable concept might be that puberty is reached at some pre-determined proportion of mature body size. This embraces the notion that animals have different mature sizes and it explains how attainment of puberty ia associated with slower growth in some cases and faster growth in others. For example, Price et al. (1981) showed that, in a genetically mixed group of gilts, those which were regarded as genetically inferior grew more slowly between 25 and 109 kg and reached puberty earlier at a lighter weight. Within this subgroup of genetically inferior animals, the faster growing ones reached puberty earlier at a heavier weight. Similarly, in cattle, sheep and goats there are genotypes with different mature sizes. When compared at the same body weight, smaller genotypes are found to be slower growing, fatter, and at a higher proportion of their mature size than larger genotypes. If animals reach puberty at a specified proportion of their mature size then smaller genotypes would be expected to reach puberty earlier than larger genotypes when they are lighter. Similarly, for any particular genotype, faster growth induced by a higher food intake will be associated with animals that will be younger, heavier and fatter at puberty than their slower-growing counterparts.

This has led to the notion that animals need a certain amout of fat in their bodies before puberty is reached. For ewe lambs this does not seem to be the case (Moore et al. 1985). Frisch (1974) analysed human populations and concluded that significant quantities of body fat were needed before puberty was reached in girls. Kirkwood and Aherne (1985) reviewed the literature and suggested that a certain amount of body fat is required before puberty can be attained in pigs. King (1989) manipulated the body composition of gilts and studied the onset of puberty without confounding it with body weight and genotype. He selected pigs at 28 days of age and fed them diets with different protein to energy ratios to induce differences in body composition. When they were 164 days old the pigs were either heavy (101 kg) or light (71 kg) and had either low or high relative fat content. Heavier animals reached puberty before the lighter ones and the leaner animals reached puberty earlier than fatter ones suggesting that lean mass is a more important determinant of puberty than some critical level of fat.

Table 1. Body composition at age 164 days and subsequent puberty (after King 1989)

Body composition				
Liveweight (kg)	70.6	71.5	101.3	100.0
Backfat (mm)	11.3	20.9	21.7	27.2
Age at puberty (days)	193	203	179	187

Further support to rule out fatness as a major determinant of the onset of puberty comes from recent experiments of Magowan (unpublished data) who manipulated the growth of gilts by controlling their food intake. His control was a group of gilts which he fed ad libitum from 50 kg liveweight and they reached puberty very early as anticipated at 172 days of age when they weighed 108 kg and had 17.1 mm of backfat. He maintained another group of gilts at 50

kg liveweight and none of these attained puberty by 270 days of age but, when changed to ad libitum feeding, they reached puberty 65 days later when they were 335 days old. These gilts had very little fat (5.3 mm) at puberty. Similarly, when gilts were maintained at 80 kg liveweight until 270 days of age and then returned to full feeding they also reached puberty with very little body fat (6.7 mm). Even the gilts that were restricted to 85% of ad libitum from 50 kg liveweight were lean (9.6 mm) when they reached puberty at 238 days of age (Table 2).

Table 2. Age, weight and backfat at puberty for gilts fed ad libitum (AL), restricted to 85% of ad libitum from 50 kg live weight (R50), or fed to maintain weight of 50 kg (M50) or 80 kg (M80) liveweight and returned to ad libitum at 270 days of age. (from Magowan 1992)

	M50	M80	R50	AL
Nº of gilts	12	12	12	12
Age (days)	335^a	269^b	238^c	172^d
Liveweight (kg)	88^a	84^a	104^b	108^b
Backfat (mm)	5.3^a	6.7^b	9.6^c	17.1^d

The relative unimportance of body fat in the attainment of puberty is also demonstrated in the work of Britt et al. (1988) who induced gilts to stop regular oestrous cycles by restricting their energy intake. The return to cyclicity after realimentation was associated with an increase in weight gain but no increase in backfat depth.

The conclusion is from the evidence above that prolonged undernutrition will not delay puberty indefinitely and that underfed gilts reach puberty at lighter weights with proportionately less fat than well-fed animals. Protein mass or its metabolic correlates rather than adiposity have the greatest influence on attainment of puberty. Similar relationships probably exist in other species.

(a) Ovulation rate

Feeding animals to increase ovulation rate (flushing) is one of the oldest and most widely used techniques in animal husbandry. It has been used in Europe for 100 years to increase the lambing performance of sheep (Marshall 1903) and had been used in pigs for at least 50 years to increase litter size (Anderson and Melampy 1972).

In sheep, live weight and ovulation rate are usually correlated. Up to a threshold weight which depends on genotype, ewes may not ovulate at all (Fletcher 1971) but beyond this there is an almost linear relationship between live weight and ovulation rate (Edey 1968; Morley et al. 1982) until a plateau is reached that represents the genetic potential of the animal. Coop (1966) distinguished between two effects of nutrition on ovulation rate - a long-term effect of nutrition which is reflected by differences between animals in live weight (the so-called "static effect"), and a short-term effect of nutrition (3 weeks) measured by live-weight gain (the "dynamic effect"). Lindsay (1976) linked the static and dynamic effects together and hypothesised that they were part of a continuum where ovulation rate is controlled by the "net nutrient status" or the sum of the endogenous nutrients from body reserves and the exogenous nutrients from the diet.

Later work has shown that ovulation can respond to nutrition even more rapidly than proposed by the dynamic effect. Oldham and Lindsay (1984) stimulated ovulation rate in 4-6 days when they fed ewes lupins and demonstrated an immediate response of ovulation to

nutrition. Smith and Stewart (1990) have extended Lindsay's (1976) proposal and suggested that the three effects of nutrition (static, dynamic and immediate) are all part of one continuum.

The static, dynamic and immediate effects of nutrition on ovulation described above for sheep have not been demonstrated as clearly in pigs perhaps because intensively housed animals have not been subjected to the same degree of nutritional variation as grazing animals. However there are similarities between sheep and pigs. For example, increasing the level of food or energy intake during the rearing period will increase the ovulation rate at puberty (den Hartog and van Kempen 1980; Aherne and Kirkwood 1985). This is akin to the static and dynamic effect. It is also well established that short-term, high level feeding during the oestrous cycle increases ovulation rate. Anderson and Melampy (1972) and den Hartog and van Kempen (1980) reviewed a large number of experiments on flushing of gilts and sows and concluded that feeding for 11-14 days gave the most consistent response. More recently Cox et al (1987) have demonstrated that, if timed correctly in the follicular phase, flushing for as little as 5 days (similar to the lupin effect in ewes) will increase ovulation rate.

III. PREGNANCY

Nutrition during pregnancy affects reproduction in several ways. First, it may cause embryonic or fetal loss early in pregnancy from too little or, possibly, from too much food. Second, throught its effect on growth of the fetus during the later stages of pregnancy, poor nutrition can reduce survival of offspring because of low birth and, at the other extreme, too much food can cause dystocia and hence reduce reduce survival. Third, nutrition during the later stages of pregnancy may affect the growth and development of the udder and so affect the amount of milk in lactation.

(a) Embryo survival

Undernutrition has to be very severe to threaten the viability of embryos in both sheep (Edey 1966; Blockey, Cumming and Baxter 1974) and pigs (Pond et al. 1968; Speer 1982). Once an ovum is fertilized the embryo is given a very high priority in nutrient supply.

There are several reports that overfeeding in early pregnancy increases embryo mortality in sheep (El-Sheikh et al. 1955; Foote et al. 1959; Rhind et al. 1984; Parr et al. 1987). With the exception of the study by Parr et al. (1987) who imposed treatments after ovulation, the poor survival of embryos was associated with a high ovulation rate that was induced by the high level of feeding. There was little effect on the number of lambs born. Similarly in pigs high levels of feed during rearing or in the premating period are associated with an increase in embryo mortality (Table 3) but the numbers of embryos at 25 days of gestation remain the same.

Table 3. Level of feeding and embryo survival in gilts (adapted from den Hartog and van Kempen 1980)

Period	Nº of Trials	Energy intake (MJ ME/day)	Nº of embryos at 25 days	Embryo survival (%)
Prepubertal	19	35.7	9.8	69.7
	46	22.8	10.0	77.5
Premating	36	38.5	10.1	73.2
	31	21.6	9.7	78.3

More recently, Hughes (1989) has re-examined several experiments and chosen only those where the level of feeding before mating (and hence ovulation rate) was standardised between treatments. He concluded that high levels of feeding in early gestation may be detrimental to embryos even when ovulation rates are similar (Table 4).

Table 4. Effect of level of feeding in early gestation on embryo survival in sows. (summary of 12 experiments with feed intake standardised before mating) (after Hughes 1989)

	Feeding level in gestation	
	High	Low
Ovulation rate	15.4	15.5
Nº of viable embryos	11.8	12.7
Embryo survival (%)	77	82

It is strange that high levels of food in early pregnancy should reduce embryo survival. Perhaps the metabolic control system of the animal perceives high intakes of food early in pregnancy as a reflection of low reserves of body energy which are essential towards the end of pregnancy and during lactation and it responds accordingly by reducing the number of embryos.

There is also a danger in drawing conclusions from experiments that were not designed to test the hypothesis in question. In two recent experiments in Canada designed specifically to test whether excess food increases embryo mortality, no evidence could be found in gilts or sows. In the first experiment 48 gilts were given high or low intakes of energy or protein from three days after mating until day 28 of gestation. Ovulation rate and embryo survival was the same among treatments (Table 5).

In a second experiment sows were fed either 3 or 6 kg of food during lactation, fed a standard amount (2.5 kg) from weaning until 2 days after mating and then offered either 1.8 or 3.6 kg until slaughter at day 25 of gestation. Again there is no evidence from this experiment that high levels of food in early gestation increase embryo mortality (Table 6).

Table 5. Effect of energy and protein intake in early gestation on embryo survival. (from Pharazyn and Aherne 1989)

Energy Intake Protein Intake	Low Low	Low High	High Low	High High	±SE
Food intake (kg/d)	1.8	1.8	2.8	2.8	
Energy intake (MJ DE/d)	24.7	24.7	40.2	40.2	
Protein intake (g/d)	207	364	207	364	
Nº of corpora lutea	13.7	15.1	14.2	14.8	0.60
Nº of embryos	12.2	12.8	12.4	11.6	0.55
Embryo survival	85.7	88.9	85.6	80.2	3.80

Table 6. Effect of feed intake during lactation and gestation on the number of embryos and their survival. (after Baidoo 1989)

Feed intake (kg/day): Lactation	6		3		
Gestation	3.6	1.8	3.6	1.8	±SE
Nº of sows	28	28	25	24	
Nº of embryos	13.8[a]	14.5[a]	13.1[a]	11.5[b]	0.43
Embryo survival	80.6[a]	84.6[a]	75.8[b]	67.4[c]	2.41

(b) Maternal energy intake and birth weight

Nutrition during pregnancy influences reproduction through its affect on birth weight which is related to neonatal survival by a U-shaped curve (Alexander, 1984). Low birth weights are associated with low energy reserves and lowered thermoregulatory capability and hence increased perinatal mortality. High birth weights are often associated with higher mortality because of dystocia (Curll et al. 1975).

There is considerable controversy about the most appropriate way to manage the feeding of animals during pregnancy. Most of the strategies are based on the immediate demands of the the fetus at the time of feeding and, since the fetus completes two thirds of its growth in the last timester of gestation, most emphasis has been placed on this stage. Poor nutrition in late gestation is the most common cause of low birth weights and, of the important domestic animals, the ewe is the most sensitive and the sow seems the least sensitive (Ferrell 1991). Differences in body reserves between ewes and sows might explain the perceived difference in sensitivity to nutrition or it may reflect the difference in physiological age at birth because piglets are less developed at this stage than lambs (Taylor and Murray 1987).

Overfeeding in late pregnancy, particularly of animals in relatively poor condition, increases the size of the fetus over that in control animals. Unfortunately, it may do so to an extent that can cause significant reproductive losses by distochia (Curll et al. 1975).

The influence of nutrition on fetal growth is not just confined to late pregnancy. Through its effects on placental growth, nutrition can effect the development of the conceptus and hence birthweight at any stage of pregnancy and this will be discussed in detail in a later paper in this proceedings (Kelly, 1992).

(c) Growth of the udder

Growth of mammary tissue begins during fetal life and continues throughout postnatal life both before and after puberty, but most development takes place during pregnancy or immediately thereafter (Forsyth 1989). Mammogenesis and milk production can be impaired by either underfeeding or by overnutrition. A curious but important observation was made by Little and Kay (1979) who found that milk production was depressed if dairy heifers were reared on a high plane of nutrition to reduce the age at puberty. Detrimental effects of high levels of feeding before puberty have also been found in sheep (Johnsson and Hart 1985) and beef heifers (Johnsson and Obst 1984).

Nutrition during pregnancy can have marked effects on milk production of farm animals because most of the development of the alveolar (secretory) cells takes place during this stage. In sheep, a reduction in food intake during pregnancy reduced mammary growth to about the same extent

as fetal growth (Rattray et al. 1974) and reductions in mammary weight are associated with reductions in the amount of colostrum and subsequent milk production for the first 24 hours of lactation (Mellor et al. 1987). In pigs we have manipulated nutrition in pregnancy and changed the lean to fat ratio in the maternal gain but kept total gain in maternal weight constant. The density of secretory cells was doubled in animals with the higher lean to fat ratio but all other components of the mammary gland remained the same, that is, the total gland weight was the same and the proportions of tissues within the gland (alveolar wall, alveolar lumen, adipose tissue, and connective tissue) remained unchanged (Head and Williams 1991). Further, we have shown that this increase in secretory cell density is associated with large increases in milk production (Head and Williams 1992, unpublished).

IV. LACTATION

The onset of lactation makes a very sudden and large metabolic demand on the mother but the response in appetite is slow so that maternal tissues have to be mobilised to meet the shortfall. Thus, the energy balance of the mother is negative for about the first third of lactation which corresponds to five or six weeks in pigs and about 100 days in dairy cows. Evidence is accruing that it is energy balance which controls when the next reproductive cycle will begin.

(a) Lactational (or post-partum) anoestrus

Provided ewes are within their breeding season, lactation and suckling will usually delay the resumption of cyclical oestrous activity after parturition. This phenomenon is lactational anoestrus. Lactation itself imposes a severe nutritional stress on the ewe and suckling may exacerbate the effect because it often promotes a high level of lactation. It has been suggested that this nutritional stress alone accounts for lactational anoestrus because, lactating ewes fed to meet their estimated nutritional demands show no delay in returns to cyclical activity compared to ewes whose lambs had been weaned at 24 hours (Hunter & Van Aarde 1973). However, a number of other authors have suggested that lactation and lactation plus suckling prolong the interval from parturition to oestrus in ewes that are not nutritionally stressed (Restall 1971; Shevah et al. 1974). This controversy probably arises from the use of different breeds, different estimates of nutritional requirements and different levels of nutrition during pregnancy.

Pigs differ from sheep, cattle and goats because they will not exhibit oestrus during lactation if they are lactating well and suckling a normal-sized litter. Traditionally, this has not posed any constraints on reproductive performance or herd management because sows have always had the potential to resume normal cyclical activity within a week of weaning, provided weaning takes place at least three weeks after parturition. In recent years, however, anoestrus after weaning has become a more common reproductive disorder and has been recognised in Europe, North America and Australia (Hurtgen et al. 1980; Reese and Moser 1981; Karlberg 1980; King et al. 1982). These studies are remarkably consistent and show that 20% of multiparous sows fail to exhibit oestrus in the first week after weaning. The problem is even worse in first-litter sows where up to 50% fail to exhibit oestrus within a week of weaning.

Inadequate nutrition of sows during their first lactation has been implicated as a major factor in post-weaning anoestrus (Reese et al. 1982; King and Williams, 1984) but this depends on the body reserves of the animal. For example, in first-litter sows that weigh about 140 kg after farrowing, a loss of 20 kg will increase the interval between weaning and remating. In contrast, heavier animals can afford to lose more in lactation before their fertility is reduced. In sows weighing 170 kg at the start of lactation, the interval from weaning to mating was not affected by a loss of 30 kg but was increased when the loss reached 45 kg (Mullan and Williams

1989). This implies that there is a critical weight at weaning below which fertility is impaired. King (1987) suggested that the protein mass of the sow at weaning was the best predictor of the interval from weaning to oestrus. He points out that multiparous sows are more resilient to nutrient restriction in lactation and, although they often have less fat than first-litter sows, they have greater body reserves. We have manipulated the protein mass of first-litter sows at weaning by changing their diet (Table 7). The clear message from these data is that even sows with very small amounts of protein at weaning (less than 14 kg lean) still return to oestrus after weaning in a reasonable time. This suggests that the animal monitors not its body weight or protein mass per se but some other variable such as the rate of loss of body reserves or its energy balance. Sows are normally weaned when their piglets are between 3 and 4 weeks of age and, as pointed out earlier, this means that they are expected to begin re-breeding when they are likely to be still in negative energy balance.

Table. 7. The interval from weaning to mating, body weight and body protein at the start of lactation and at weaning for heavy (H) and light (L) gilts with high (h) or low (l) body protein at the start of lactation (after Williams and Smits 1991)

	Hl	Hh	Ll	Lh
Nº of gilts	27	36	33	39
After farrowing				
Body weight (kg)	161	162	150	150
Body protein (kg)	16.7	21	15.5	19.0
At weaning (30-day lactation)				
Body weight (kg)	134	139	127	136
Body protein (kg)	15.1	19.1	13.5	16.8
Interval from weaning to mating (d)	15.3	14.1	14.7	14.0

There seems little doubt that the voluntary food intake of modern-day sows is less than that of their counterparts of twenty years ago and that the change is associated with selection programmmes aimed principally against backfat. For example, Lodge (1962) observed that first-litter sows rarely had difficulty in eating 7.3 kg daily, but more recent estimates of the potential intake of food are much lower. After an extensive review of voluntary food intake, Mullan et al. (1989) suggested that the average daily intake for first-litter sows is 4.5 kg and that they reach a maximum of 5.5 kg daily after four weeks. These intakes are for sows kept under experimental conditions - in commercial situations, the estimates for the mean intake during lactation are far lower - for example, 3.1 kg (King et al. 1982) and 2.9 kg (Cox et al. 1983). Not only is food intake of sows now lower but their potential milk output is higher (King et al. 1989) than sows of twenty years ago and this means that they are likely to be in negative energy balance for longer.

Dairy cattle are similar to pigs because their ovarian activity after parturition also seems to depend directly on energy balance or the availability of nutrient energy relative to its utilization for lactation (Butler and Elrod 1991). The highest milk producers are generally those animals in greatest energy deficit and they take the longest to return to normal ovulatory activity. First-calf heifers exhibit a longer delay in the resumption of normal activity than mature cows.

As pointed out earlier in this section, mobilization of maternal tissue during lactation is a necessary and perhaps unavoidable part of the reproductive cycle. However, the demand for more and more production from our animals in modern commercial herds gives them little opportunity to accumulate body reserves in the way they did under traditional, less intensive systems of management. The corollary is that we have reduced the capacity of the animal to

buffer short-term changes in the energy supply and this has made the reproductive system more sensitive to nutrition.

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