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A review of nutritional influences on reproduction in boars, bulls and rams

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Summary — In this paper, nutritional influences on reproduction in boars, bulls and rams during prepubertal life and in the adult is reviewed. Reproductive functions in young animals appear to be more susceptible to dietary restrictions of energy and protein than in the adult and severe feed restriction may even result in permanent damage to gonadal and neural tissue. Whilst restricted feed intake in adult animals can reduce androgen secretion and semen quality, such effects are temporal as re-feeding previously underfed adult animals usually restores reproductive function. There is now considerable evidence suggesting that the influence of nutrition on reproductive processes is mediated *via* effects of dietary constituents on the hypothalamic-pituitary axis, although there is some indication that dietary changes may affect the testis directly. That some nutritional regimes imposed on animals can alter volume of ejaculates and androgen activity without necessarily affecting spermatogenesis, suggests that certain constituents of the diet can differentially affect the production and/or the release of LH and FSH.

nutrition / reproduction / male / farm animals

Résumé — Influence de la nutrition sur la reproduction mâle chez les porcins, les ovins et les bovins. Cet article analyse les effets du régime alimentaire sur la reproduction des verrats, taureaux et béliers au cours de leur vie prépubère et adulte. La fonction de reproduction semble plus sensible aux restrictions d'énergie et de protéines chez les jeunes animaux que chez les adultes. Une restriction alimentaire sévère peut même produire des dégâts permanents au niveau des gonades et du tissu nerveux. Une alimentation restreinte des animaux adultes peut réduire la sécrétion des androgènes et la qualité de la semence. Toutefois ces effets sont transitoires car la réalimentation d'animaux adultes antérieurement mal nourris restaure leur fonction de reproduction. De nombreux arguments suggèrent aujourd'hui que l'influence de la nutrition sur la reproduction s'exerce par l'intermédiaire des composants du régime alimentaire au niveau des centres hypothalamo-hypophysaires, même si certains résultats indiquent que les changements d'alimentation ont une action directe sur le testicule. Certains régimes alimentaires donnés aux reproducteurs peuvent changer le volume de sperme produit ainsi que la production des androgènes, sans nécessairement affecter la spermatogénèse. Ceci suggère que certains constituants de l'alimentation peuvent agir différemment sur la production et/ou la sécrétion des hormones LH et FSH.

nutrition / reproduction / mâle / animaux domestiques

INTRODUCTION

The effects of nutrition on mammalian reproduction have been the subject of many reviews (eg, Blaxter, 1956; Lamming, 1969; Allden, 1970; Leathem, 1970; Dziuk and Bellows, 1983; Kemp and Den Hartog, 1989; Lindsay *et al*, 1990). The purpose of this paper is to review the nutritional factors that are known to influence reproduction in boars, bulls and rams, with particular emphasis on dietary components such as energy and protein that affect onset of puberty, expression of libido, testicular function and endocrinology. Certain chemical substances in some feeds can result in poisoning, and deficiencies in nutrients, such as water, dietary vitamins or minerals, can also exert deleterious effects on normal reproductive function (Underwood and Somers, 1969; Leathem, 1970; Short and Adams, 1988) but as these substances have been extensively reviewed elsewhere, they will not be considered in the present paper.

It is generally accepted that nutritional management is the main limiting or controlling factor for reproduction in many types of domestic livestock (Short and Adams, 1988). Since domestic ruminants in many parts of the world are grazed on pasture and are bred by natural service, the quality and quantity of the available feed, particularly in the period leading up to joining, are crucial for successful mating and subsequent fertilization. Pasture, however, is not always able to maintain a high rate of fertility in breeding stock due to seasonal changes in feed supply. Consequently, grazing animals encounter qualitative and quantitative deficiencies in the diet at some time each year, which can have marked effects on reproductive efficiency (Gunn *et al*, 1942). Indeed, the seasonal variation in testis size and body weight of Merino rams grazing pastures in the Mediterranean environment in south-western Australia is well documented, an effect that appears to be independent of

photoperiod (Masters and Fels, 1984). As testicular size has a positive correlation with the capacity to produce sperm (Oldham *et al*, 1978; Martin *et al*, 1987), it is not surprising that seasonal variation in sperm production also occurs. However, in regions in the northern hemisphere with a temperate climate, such seasonal effects on male reproduction are more influenced by changes in photoperiod than by nutrition. Superimposed upon these recurrent and short-term seasonal variations in feed supply are the occasional, prolonged periods of severe undernutrition during drought or flood. Accordingly, an understanding of the effects of nutrition *per se*, as well as specific effects of nutrition on the reproductive performance of farm animals during times of feed scarcity, is of economic importance for, even under the harshest of environmental conditions, nucleus herds or flocks must be maintained and managed at the lowest cost possible.

In practice, energy conservation mechanisms in animals balance out fluctuations in dietary supply by restoring body reserves during periods of feed surplus and mobilizing these body reserves during periods of scarcity (Allden, 1970). During energy deficit, the energy balance is not negative, even if the animal is mobilizing body reserves. Thus, there is a need for a constant supply of dietary amino acids, vitamins and energy for basic tissue maintenance, thermoregulation and the locomotor demands of foraging (Hervey, 1971). Once these demands are met, the remaining energy can be allocated to growth and reproduction.

Although the mechanism by which undernutrition affects testicular function is not fully understood, it has long been recognized that this process is mediated, at least in part, by the anterior pituitary gland (Jackson, 1925; Mason and Wolfe, 1930; Mulinos and Pomerantz, 1941; Samuels, 1950; Srebniak and Nelson, 1962; Root and Russ, 1972; Stewart *et al*, 1975; Millar and Fairall, 1976).

From studies on prisoners of war, who developed gynecomastia and suffered from reduced testicular function as a result of prolonged, severe malnutrition, Klatskin *et al* (1947) and Salter *et al* (1947) suggested that the restriction of food produced effects either directly on the testis or indirectly via the pituitary, with a resultant decrease in androgen or "inhibin" activity. Indeed, in more recent studies, nutrition has been shown to exert quite marked effects on gonadotrophin secretion (Martin *et al*, 1989). However, the exact mechanisms involved in the direct effects of different planes of nutrition on testis function, particularly in regard to the response of androgen target tissues such as the seminiferous tubules, remain elusive.

NUTRITIONAL STATES IN ANIMALS

Provided the intake is correct, an adequate diet is one in which the balance of nutrients in the diet will maintain normal health and function (Jöchle and Lamond, 1980). For domestic animals, such a diet is referred to as maintenance requirements and supports a condition of nitrogen and carbon equilibrium. On the other hand, production requirement is the amount of food needed to produce an increase in growth, milk or wool production, or an expected level of work for any individual animal (Tribe and Cumming, 1955). Thus, the type and composition of the required end product is an important factor in determining the type of nutrients that must be supplied to the animal in food.

Deficiencies in the quantity of food available, but not necessarily the quality, leads to undernutrition (Reid, 1990). Hence, undernourished animals are those that do not receive sufficient amounts of an adequate diet to meet specific requirements such as pregnancy, lactation or sperm production. Undernutrition, therefore, is primarily an energy deficiency and because it is a

disease (from a nutritional view point) associated with loss of body weight, undernourished animals are at risk. In the literature, several terms such as undernutrition, under-feeding, restricted feeding, sub-maintenance or low energy intake are used to describe the nutritional limitations placed on animals which ultimately result in the animal being in an undernourished condition.

In contrast, malnutrition is a disease which occurs when the quality of food available, but not necessarily the quantity, is inadequate to meet requirements (Reid, 1990). More specifically, it constitutes food deficiencies of protein, essential amino acids or fatty acids, minerals or vitamins, or may be due to chemical imbalances which prevent the animal from utilizing certain essential nutrients. Inanition in animals is characterised by a state of physical exhaustion, which is caused by lack of nourishment or the inability to assimilate food and may arise through prolonged undernutrition or malnutrition.

In practice, there is no reason why any such deficiencies should occur in hand-fed domestic livestock such as pigs, as trace elements and vitamins are routinely incorporated in proprietary feed mixtures. The situation in the grazing animal, however, is quite different as deficiencies in the intake of nutrients can occur.

INFLUENCE OF NUTRITION DURING PREPUBERTAL LIFE ON GROWTH AND SEXUAL DEVELOPMENT IN MALES

Although the attainment of puberty in the first breeding season is less important in the male than in the female for determining future productivity, it could be important in selection programs designed to shorten the generation interval. Puberty, however, has been difficult to define because as it does not necessarily represent a specific time in life. Rather, it is a period during which matu-

ration of various physiological, biochemical and behavioural processes occur that, in males, support completion of spermatogenesis, expression of libido and accomplishment of normal ejaculation. Nevertheless, it is agreed that puberty in larger domestic animals, and in man, is not synonymous with sexual maturity or adult status, which occurs months or even years later (Amann, 1981) when full reproductive capacity is attained.

In general, immature animals are more susceptible to nutritional deficiencies in terms of reproductive effects than the adult and, in some circumstances, may suffer permanent damage to the reproductive function (Ferrell, 1991). In prepubertal life, the result of undernutrition is generally to retard sexual development, delay the time of onset of puberty, retard the appearance of the external genitalia and suppress spermatogenesis (Mason, 1939; Anderson, 1945; Spies, 1958; Bratton *et al*, 1959; Reid, 1960; Baronos *et al*, 1969; Leathem, 1970). It appears that Sertoli cells and the proliferation of undifferentiated germ cells and spermatogonia may not be significantly impaired, though the latter germ cells can be affected after extreme undernutrition (Mason, 1939). Differentiation of the more mature germ cells may be inhibited (Siperstein, 1921; Jackson, 1932), as was evidenced in young rats underfed from 3 weeks of age, in which spermatogenesis was arrested at the primary spermatocyte stage for up to 400 d (Siperstein, 1920).

Boars

With boars, age appears to be more important than body weight in determining the onset of puberty, which occurs in most breeds at approximately 200 d of age (Rat-tray, 1977). An exception appears to be breeds of Chinese pigs, including Meishan, Jinhua, Dahuabai and miniature types such

as Bama Xiang, all of which attain puberty closer to 100 d than 200 d of age (Kato and Harayama, 1990; Lang *et al*, 1992; Liu *et al*, 1992; Wang *et al*, 1992). In general, maintaining boars on low planes of nutrition for various lengths of time from weaning resulted in a delay in body and testicular growth and impairment to development of testicular cells and spermatogenesis (table I).

Phillips and Andrews (1936) and Niwa (1954) reported that the reduction division of spermatocytes was delayed in underfed boars, with secondary spermatocytes appearing in the germinal epithelium approximately 4–6 weeks later than in normal-fed controls. Furthermore, spermatozoa collected from the cauda epididymis of the underfed boars were inactive at 5 months of age and, while normal motility of spermatozoa was generally in evidence by 7 months, some of the underfed animals still had no spermatids at 10 months of age (Niwa, 1954). Severe underfeeding of young boars from 2–3 weeks of age for 1 yr (Dickerson *et al*, 1964) resulted in even more serious effects on the testis (table I). These workers reported that the cytoplasm of the interstitial cells had begun to shrink from 1 month after undernutrition commenced and had disappeared after 3 months on the restricted diet. From that time, it was impossible to distinguish the nuclei of likely interstitial cells from those of lymphocytes (Dickerson *et al*, 1964). Upon re-feeding, spermatogenesis developed much more rapidly than did the reappearance of Leydig cells, which ultimately developed in normal amounts once the pigs reached 120 kg liveweight.

Protein-energy (calorie) deficient feeding of boars from about 3 weeks of age (Platt and Stewart, 1967) resulted in marked, and possibly, permanent damage to the testes even after 40–50 d on the diet. The most distinct changes were evident in the interstitial cells (Leydig cells) in which the cyto-

Table 1. Effects of low planes of nutrition on growth and reproductive development of young boars, changes relative to normal-fed controls.

<i>Observation</i>	<i>Reference</i>
Body growth retarded	Phillips and Andrews (1936) ^a Dutt and Barnhart (1959) ^b
Testicular growth retarded	Phillips and Andrews (1936)
Testicular morphology impaired development of Seminiferous tubules Germinal epithelium Tunica dartos muscle Interstitial cells	Niwa (1954) ^c ; Dickerson <i>et al</i> (1964) ^d Phillips and Andrews (1936) Phillips and Andrews (1936) Dickerson <i>et al</i> (1964)
Spermatogenesis Reduction division of spermatocytes delayed No spermatogenesis Sperm motility impaired for up to 10 months	Niwa (1954) Dickerson <i>et al</i> (1964) Niwa (1954)

^a Low plane of nutrition from weaning; ^b boars fed from weaning for 312 d at 70 and 50% of the standards recommended by the US National Research Council, *ie* a ration of yellow maize (75%), soya bean meal (22%), minerals and vitamins with a crude protein content of 16%; ^c undernutrition from weaning; ^d undernutrition from 2–3 weeks of age for 1 yr.

plasm was markedly reduced. In these cells, the diameters were only 1/2 to 2/3 those of the controls and the nuclei were small and crowded together. This effect on the Leydig cells persisted beyond puberty and was apparent in older boars that had been maintained on this diet, despite the fact that their testes had undergone a 'spectacular' increase in size. Presumably, such testicular growth was due to an increase in length and diameter of the seminiferous tubules, many of which at this stage had developed a lumen and contained numerous spermatocytes but few spermatids (Platt and Stewart, 1967). Also, it appeared that the protein-calorie deficiency produced detrimental effects on may endocrine glands, including the pituitary (see later section on gonadotrophins), such that the morphological changes observed in the anterior lobe were consistent with impaired hormonal secretion.

Bulls

In contrast to boars, the onset of puberty in bulls appears to be influenced more by body weight than by age (Alliden, 1970; Dyrmondsson, 1973; Young, 1974; Rattray, 1977). However, other findings indicate that body weight and age at puberty are influenced by level of nutrition and post-weaning rate of gain (see Ferrell, 1991). In general, dairy and beef breeds maintained on low planes of nutrition (James, 1950; Davies *et al*, 1957; Flipse and Almquist, 1961; VanDemark *et al*, 1960; Hiroe *et al*, 1964; VanDemark and Mauger, 1964; Almquist, 1982; Gauthier and Berbigier, 1982) from birth or weaning for periods up to 7 yr, grew at a slower rate and therefore attained puberty later than their normal-fed or high-plane counterparts, as evidenced by delayed development of the testes, the seminal vesicles, the ampullae and the epididymides

Table II. Effects of low planes of nutrition on growth and reproductive development of young bulls, changes relative to normal-fed controls.

<i>Observation</i>	<i>Reference</i>
Testicular growth retarded	Davies <i>et al</i> (1957) Pakenas and Pilipaviciute (1966)
Development of seminal vesicles (ampullae, epididymides) retarded	Davies <i>et al</i> (1957)
Testicular morphology impaired development of:	
Seminiferous tubules	Davies <i>et al</i> (1957)
Tunica dartos muscle	Phillips and Andrews (1936)
Interstitial cells	Davies <i>et al</i> (1957)
Germinal epithelium unaffected	Bratton <i>et al</i> (1959)
Ejaculate volume reduced	Davies <i>et al</i> (1957); Flipse and Almsquist (1961) Hiroe <i>et al</i> (1964) VanDemark <i>et al</i> (1964)
Spermatogenesis	
Sperm production reduced	VanDemark <i>et al</i> (1964) Pakenas and Pilipaviciute (1966)
Sperm morphology unaffected	James (1950); Pakenas and Pilipaviciute (1966)
Sperm motility reduced temporarily	Flipse and Almquist (1961) Pakenas and Pilipaviciute (1966)

and a reduction in the volume of ejaculates (see table II). Additionally, seminal concentrations of fructose, total nitrogen, ascorbic acid and acid-soluble phosphorus as well as calcium are also reduced in bulls fed low-plane diets (Hiroe *et al*, 1964).

On the other hand, whilst the higher energy diets advanced puberty and hastened testicular development and function (see table III), it did not enhance ultimate testis size (Almquist, 1982). These findings conflict with those of Pruitt *et al* (1986), who concluded that higher levels of dietary energy fed to Simmental and Hereford bulls from weaning (about 211 d of age) did not hasten sexual development (as assessed from testosterone concentrations), age at first mating or age at puberty. These workers claimed that the energy levels fed to the animals (low 3.2–3.5, medium 4.2–4.6 and high 5.3–5.7 MJ metabolizable energy (ME) per bull daily) may not have been large enough to affect endocrine changes that had begun several months before the com-

mencement of the trial. However, an alternative explanation is that these animals had already reached puberty since they were 211 d of age at the outset of the trial. Continuous overfeeding or intensive feeding of young bulls can result in lowered reproductive performance (Schilling and Krajnc, 1964; Young, 1974; see table III). In such over-fed animals, it is possible that additional scrotal lipid and/or deposition of fat around the pampiniform plexus resulting from high energy (concentrate) diets, may impair thermoregulation of the scrotal contents thereby reducing epididymal sperm reserves (Coulter and Kozub, 1984) and presumably sperm production. However, in such a circumstance, it is likely that morphological abnormalities in spermatozoa in the ejaculates would also be encountered.

Severely reducing protein (from 8.09 to 1.35%) in the diet of young beef bulls, by either a progressive reduction over many months or instantly to a level of 1.61% (Mecham *et al*, 1963), or by feeding protein-free

Table III. Effects of high energy diets or continuous overfeeding on growth and reproductive development of young bulls, changes relative to normal-fed controls.

<i>Observation</i>	<i>Reference</i>
Body growth increased	Schilling and Krajnc (1964) ^a
Testicular growth increased	Almquist (1982) Pakenas and Pilipaviciute (1966) Schilling and Krajnc (1964)
Development of seminal vesicles (ampullae, epididymides):	
Hastened	Davies <i>et al</i> (1957)
Reduced	Schilling and Krajnc (1964)
Testicular morphology impaired development of :	
Seminiferous tubules	Davies <i>et al</i> (1957)
Tunica dartos muscle	Phillips and Andrews (1936)
Interstitial cells	Davies <i>et al</i> (1957)
Germinal epithelium unaffected	Bratton <i>et al</i> (1959)
Ejaculate volume reduced	Davies <i>et al</i> (1957); Flipse and Almquist (1961) Hiroe <i>et al</i> (1964) VanDemark <i>et al</i> (1964) Schilling and Krajnc (1964)
Spermatogenesis	
Sperm production:	
Increased	Almquist (1982)
Reduced	Schilling and Krajnc (1964)
Sperm morphology:	
Unaffected	Hentges <i>et al</i> (1964)
Abnormalities	Mwansa and Makarechian (1991)
Sperm motility increased	Almquist (1982)
Epididymal sperm reserves reduced	Coulter and Kozub (1984)

^a Continuous overfeeding of bull calves from 3 weeks of age for 1 yr.

(urea-containing) diets to young beef bulls for several years (Johnson *et al*, 1971), resulted in reduced sperm-producing capacity but had no apparent detrimental effect on sperm motility or the percentage of abnormal spermatozoa (see table IV). As the bulls on the urea-containing diet maintained normal levels of sexual activity, with the result that their subsequent fertility was unaffected, Johnson *et al* (1971) concluded that protein is not essential in the diet of beef bulls to attain normal fertility. Presumably with ruminants fed diets in which urea serves as the only source of dietary nitrogen, the ruminal microbes and the host ani-

mal itself are capable of synthesizing the nitrogenous compounds needed to support reproductive processes (Oltjen *et al*, 1971). Indeed, earlier work on underfeeding young bulls (Baronos *et al*, 1969) showed that the content of non-protein nitrogen, vitamin A and carotene in the blood of the underfed animals was no different from that of the normal-fed controls, even though the concentrations of most of the free amino acids (13 out of 16) and glucose was reduced.

Experiments which involve reversing planes of nutrition have produced some controversial results. Increasing the plane

Table IV. Effects of low-protein diets and protein-free (urea-containing) diet on growth and reproductive development of young bulls, changes relative to normal-fed controls.

<i>Observation</i>	<i>Reference</i>
Body growth retarded	Meacham <i>et al</i> (1963) ^a ; Johnson <i>et al</i> (1971) ^b
Testicular growth retarded	Johnson <i>et al</i> (1971)
Testicular morphology impaired development of:	
Interstitial cells	Meacham <i>et al</i> (1963)
Germinal epithelium	Meacham <i>et al</i> (1963)
Semen volume reduced	Meacham <i>et al</i> (1963); Johnson <i>et al</i> (1971)
Sperm number/ejaculate reduced	Meacham <i>et al</i> (1963); Johnson <i>et al</i> (1971)
Sperm motility unaffected	Meacham <i>et al</i> (1963); Johnson <i>et al</i> (1971)
Sexual activity:	
Unaffected	Johnson <i>et al</i> (1971)
Reduced ^c	Meacham <i>et al</i> (1963)

^a Protein reduced from 8.09 to 1.35% in the diet of young bulls over many months or instantly to a level of 1.61%;

^b protein-free (urea-containing) diets fed to young beef bulls for several yr; ^c lower libido associated with weakened condition rather than any actual loss of sexual desire (Meacham *et al*, 1963).

of nutrition in former low-plane-fed bulls enhanced their sperm production which proceeded at a faster rate than their increase in body weight (James, 1950). In contrast, VanDemark *et al* (1964) reported that re-feeding bull calves for 1 yr with 100% TDN, that were previously fed a low-plane diet (60% TDN) from 8 weeks to 46 months of age had no effect on improving testis growth, semen volume or sperm production, despite the fact that during the period of re-feeding, these animals grew to reach 90% of the mean body weight of the normal-fed controls. In previously protein-deficient yearling bulls, the return of the animals to an adequate diet for at least 6 weeks resulted in an increase in body weight, a recovery of normal secondary sex gland function as evidenced from their normal concentrations of fructose, citric acid and 5-nucleotidase activity and, although semen volume increased, the adequate diet did not induce an elevation in the concentration of spermatozoa (Meacham *et al*, 1963). The failure of re-feeding to induce full reproductive function in previously underfed young

animals, may reflect some degree of damage to neural centres controlling reproduction due to deficiencies in dietary components early in life or to impaired ability of the animals to synthesise adequate protein which appears necessary to facilitate the action of hypothalamic-releasing factors (Watanabe *et al*, 1968; Leatham, 1970).

Rams

An adequate plane of nutrition is also of vital importance for normal development of ram lambs and the rate of sexual development is highly dependent on the growth rate of the animal. As with bulls, growth and subsequent body weight appears to be a better guide to the onset of puberty in rams than age (Dunn, 1955; Watson *et al*, 1956; Courrot, 1962; Moule, 1970; Dymundsson, 1973; Rattray, 1977). Depending on the breed and sensitivity to photoperiodic stimulation, this body weight may vary from 40 to 70% of adult body weight (Rattray, 1977).

From controlled feeding experiments (Ragab *et al*, 1966; Pretorius and Marincowitz, 1968), it has been shown that rams reared on higher planes of nutrition attained puberty (age at which sperm first appeared in the ejaculate) at younger ages (Merino: 191.4 ± 7.1 d) and at heavier body weights (28.6 ± 1.1 kg) than rams on lower levels of feeding (Merino: 219 ± 7.7 d and 24.7 ± 0.5 kg, respectively). Further, the low-plane rations considerably delayed descent of the testicles, penile development and first appearance of spermatozoa in the ejaculate (Pretorius and Marincowitz, 1968). As these processes are androgen-dependent, it was concluded that restricted feeding had inhibited gonadotrophic hormone release which resulted in a decrease in androgen activity (Pretorius and Marincowitz, 1968).

Season of birth as well as season *per se*, through variations in feed availability, can also markedly influence subsequent growth and reproductive development of rams. However, such nutritional effects may be overridden by seasonal photoperiodism (Courot *et al*, 1975). Suffolk, cross-bred (Skinner and Rowson, 1968) and Clun Forest (Dyrmundsson and Lees, 1972) ram lambs born in late summer were found to have smaller body weights, smaller testes with seminiferous tubules of reduced diameters and secreted androgens later, than those born in spring. Spermatogenesis appeared to be unaffected by time of birth. These effects were attributable to fluctuations in nutritional conditions during rearing, with the late-summer-born lambs suffering primarily through reduced energy intake (Skinner and Rowson, 1968) and consequently affecting earliness of puberty (Dyrmundsson and Lees, 1972). However, variations in pituitary LH content due to photoperiodic effects of season (Courot *et al*, 1975) may also have contributed to differential rates of testicular growth. Young Merino rams grazing pasture in the Mediterranean environment of south-western

Australia over 13 months and raised in isolation from ewes from about 7 months of age, gained and lost testis size at a greater rate than liveweight during winter/spring and summer autumn, respectively (Masters and Fels, 1984). The 60% decrease in testis size and the loss in body weight appeared to be independent of photoperiod and was mainly associated with a decline in the energy and protein content of the pasture over summer and autumn (Masters and Fels, 1984). At this time, the nitrogen content of the pasture may be as low as 0.7 to 2.0% (Fels *et al*, 1959), which is far less than that required for maximum testicular growth (Braden *et al*, 1974; Oldham *et al*, 1978).

INFLUENCE OF NUTRITION ON REPRODUCTIVE FUNCTION IN MATURE MALES

The reproductive organs of the adult male are more resistant to dietary changes than are those of the immature animal (Leatham, 1970, 1975). In general, most of the nutritional-induced changes to reproductive function in adult boars, bulls and rams are temporary but their severity can vary from little effect on seminal characteristics and/or libido to infertility. Similarly, overfeeding of sires, as is sometimes practiced in preparation for sale or 'show', can also have detrimental effects on reproductive capacity (Skinner, 1981). Clearly, the degree of undernutrition or of overfeeding imposed as well as its duration, contributes to these disparate responses, but in most instances reproductive function returns to a normal or near-normal state upon resumption of a standard diet.

Boars

Much of the work on nutrition in mature boars has been conducted in relation to body composition and establishment of

balanced diets designed for intensive rearing. There are few studies on nutrition–reproduction interactions in mature boars. Kemp and Den Hartog (1989) concluded from their review on this subject, that energy or protein intake had little effect on libido or on sperm quality in mature boars, except when the condition of the animal became extremely poor as a result of prolonged undernutrition. Moreover, studies on the influence of protein intake on the number of sperm cells in the ejaculates of mature boars have produced contradictory results.

Stevermer *et al* (1961) fed 22-month-old Yorkshire boars on different levels of feed intake for 15.5 months. Over this period, the animals fed *ad libitum* (74.5 MJ digestible energy (DE)/d) a diet recommended by the National Research Council (NRC) for adult boars gained 136 kg, those on 100% of NRC (40.2 MJ DE/d) gained 39 kg, whilst those on low plane (initially 75%, then 50% of NRC) lost 60 kg liveweight. They found that the restricted feed intake resulted in a marked reduction in semen volume whilst full-feeding did not increase semen volume over that obtained on the medium plane of nutrition. Further, as the concentration of spermatozoa increased with decreasing volume, the number of spermatozoa per ejaculate was little affected by the plane of nutrition. This suggested that the output of the accessory glands, but not the output of spermatozoa by the testes, was affected by the reduced feed intake and is likely to reflect a suppression of androgen secretion, and therefore androgen stimulation, of the accessory glands (see later). Moreover, neither motility nor fertility (appraised from artificial insemination trials) of freshly ejaculated spermatozoa obtained from boars on the restricted diet was affected over the prolonged period. This indicated that widely varying planes of nutrition can be tolerated by adult boars without detrimental effects on spermatogenesis (Stevermer *et al*, 1961), provided they are not permitted to become physically weak.

Bulls

Restricted feeding of mature Dexter bulls over a period of 23 weeks, such that the bulls lost 6.5 kg liveweight per week had no observable effect on volume and density of semen, or motility and morphology of spermatozoa (Mann and Walton, 1953). On the other hand, feeding a low protein diet to adult bulls for about 1 yr, resulted in smaller testes and epididymides than control bulls and their gonadal and extragonadal reserves of spermatozoa were reduced to 70–75% of that for control bulls (Laszczka *et al*, 1969a,b). Though the volume of ejaculates and the percentage of live spermatozoa were also in decline after 8 months on this diet, there were no apparent morphological changes in the spermatozoa (Laszczka *et al*, 1969a). From studies in mature dairy bulls (Branton *et al*, 1947; Shirley *et al*, 1963), it appears that a concentrate mixture containing approximately 12% protein, when fed with mixed hay, will supply sufficient protein for maintenance of body weight as well as satisfactory semen production. Increasing the protein content of the diet to 20% had no additional, beneficial effect on semen quality in bulls (Shirley *et al*, 1963).

Normally, underfeeding does not affect the sexual desire of bulls unless it becomes extreme, or continues over a long period of time (Walker, 1967). However, long-term feeding of bulls on low protein rations, or overfeeding of bulls, can reduce their libido compared with that of bulls fed either normal or above normal rations (see table V).

Rams

A distinct cyclical pattern of changes in liveweight (Russel *et al*, 1976; Masters and Fels, 1984) and testis size (Masters and Fels, 1984) throughout the year is apparent

Table V. Effects of different diets on sexual activity in mature bulls, changes relative to normal-fed controls.

<i>Diet</i>	<i>Sexual activity</i>	<i>Reference</i>
Undernutrition	Unaffected ^a	Walker (1967) Wierzbowski (1978)
High energy diet	Unaffected	Mwansa and Makarechian (1991)
Low protein diet	Reduced libido ^b	Meacham <i>et al</i> (1963)
Overfeeding	Reduced libido ^c	Flipse and Almquist (1961) Hentges (1967); Walker (1967)

^a Unaffected unless underfeeding becomes extreme or continues over a long period of time; ^b reduced libido appeared to be associated with an increase in physical weakness due to emaciation; ^c lower libido appeared to be due to lack of physical strength associated with their excessive fatness. Effect on libido can be reversed on resumption of normal maintenance diet but may be permanent if animals are kept overfat beyond 2 yr.

in grazing rams, with maximum values occurring soon after the time of greatest feed production. Several studies on nutrition in rams have demonstrated that 'improved' diets result not only in heavier live-weights, but also in enhanced testis size and sperm production (Lindsay *et al*, 1976; Oldham *et al*, 1978; Martin *et al*, 1987; Cameron *et al*, 1988). However, as these diets comprised increased amounts of both digestible energy and protein, in addition to minerals and vitamins, it was not possible to determine whether specific component(s) of the diet contributed to the observed reproductive effects.

Restricted feeding of rams for 3 months, which resulted in a reduction of body fat to less than 12% of liveweight compared with 25–49% in well-fed controls, produced a decrease in testis weight, smaller seminiferous tubule diameters and lower numbers of sperm in the epididymides than in well-fed control rams (Setchell *et al*, 1965). The relative reduction in testicular weight was more severe than the decline in body weight (Setchell *et al*, 1965). The volume of ejaculates and the motility and density of the contained spermatozoa (Comstock and Brady, 1937;

Parker and Thwaites, 1972) were also markedly reduced in rams on restricted feed intake.

In a study on sperm production, in which 2 levels of dietary energy and/or protein (made resistant to ruminal degradation) were fed to mature Merino rams, Braden *et al* (1974) found that daily sperm production was unaffected by increasing protein intake alone but was significantly enhanced by increasing either the intake of energy alone or both protein and energy. They also showed that rams fed high energy diets had significantly larger testes and seminal vesicles than those on low energy diets, while the level of protein had no material effect on these parameters (Braden *et al*, 1974). Accordingly, it was concluded that a high protein intake is not essential for high sperm production in rams. Further, it was suggested that energy intake probably had no affect either on spermatogenesis or on testosterone production directly, but may influence these parameters *via* an effect on gonadotrophin secretion. Rowe and Murray (1984) and Murray *et al* (1990) also concluded from their studies on the effect of high energy and protein intakes in rams,

that digestible energy intake is the most important nutritional factor influencing testicular growth.

Nevertheless, an adequate source of nitrogen in the diet is essential to facilitate normal reproductive function and it appears that rams are able to utilize a ration with only urea nitrogen for metabolism of protein synthesis (Warnick *et al*, 1961). Feeding adult rams for 37 weeks on a diet containing about 60% of the protein comprising a standard feeding ration, Okólski *et al* (1971) reduced semen volume (54%), the total number of spermatozoa in the reproductive organs (77%) and the percentage of spermatozoa that were progressively motile (49%) compared with normal-fed control rams. Histological examinations of the testes revealed swelling and hypertrophy, atrophy of the seminal epithelium and a reduction in the number of Sertoli cells. Degeneration of some seminiferous tubules was characterised by the presence of pyknotic nuclei in some cells and numerous small vacuoles in the cytoplasm. Additionally, pathological changes were also noted in the epididymides (Okólski *et al*, 1971). A complete lack of nitrogen in the diet eventually leads to death, but rams can survive nitrogen deficiency for considerable periods without there being any detrimental effects on sperm morphology or motility, though eventually ejaculate volume and the total number of sperm cells decline (Warnick *et al*, 1961) as the testes and seminiferous tubules degenerate (Mori, 1959).

Sexual activity of rams can be influenced by nutrition but generally the effects are observed only after prolonged undernutrition and marked loss in body weight. Salamon (1964) claimed that sexual drive was more intense in rams fed a high protein than a low protein supplement. On the other hand, several workers have reported that rams fed sub-maintenance diets exhibited reduced sexual activity (Parker and Thwaites, 1972; Mattner and Braden, 1975;

Alkass and Bryant, 1984) and it was concluded that if a diet supplied adequate energy, a high protein supplement would have no beneficial effect on sexual motivation (Mattner and Braden, 1975). As underfed rams maintain an interest in oestrus ewes and mount at the first opportunity, their reduced libido appears to be more a consequence of general muscular weakness (Parker and Thwaites, 1972) rather than an effect of the restricted diet on the neural centres controlling libido. Nevertheless, the evidence suggests that when rams are not in good body condition, supplementary feeding in the 2 months prior to joining may improve their reproductive performance over the subsequent mating period through a beneficial effect on sperm output and libido, both of which can influence the coverage of oestrous ewes (Mattner and Braden, 1975).

NUTRITIONAL INFLUENCES ON REPRODUCTIVE ENDOCRINOLOGY IN MALES

It was shown many years ago that chronic inanition in mature rats resulted in complete failure of reproductive activity and an endocrine pattern resembling that in hypophysectomized animals (Mulinos and Pomerantz, 1940). Treatment of such underfed animals with chorionic gonadotrophins (rich in LH) was at least partially effective in restoring the weight and function of the reproductive organs of rats (Mason and Wolfe, 1930; Mulinos and Pomerantz, 1941; Lutwak-Mann and Mann, 1950) and bulls (Davies *et al*, 1957). Further, in underfed male rats (Mulinos and Pomerantz, 1941) and dogs (Pazos and Huggins, 1945), the accessory organs were responsive to androgen stimulation, as evidenced by their increase in weight, despite continued inadequate feeding. These studies indicate that the mechanism by which prolonged undernutrition results in testicular atrophy is

mediated, at least in part, by the anterior pituitary gland and led to the description of the condition as 'pseudohypophysectomy' (Mulinos and Pomerantz, 1941). However, these early studies could not elucidate whether undernutrition merely decreased hormone synthesis or release, or whether the observed effects were due to insufficient substrate for the target organs to function normally. From more recent studies (see below), it now appears that restricted feeding inhibits gonadotrophic hormone release with a resultant decrease in androgen activity. Further, restricted energy intake early in life may prevent or slow the maturational processes at the pituitary-hypothalamus level (Short and Adams, 1988).

Gonadotrophins

Changes in body growth and testis size of rams have been associated with seasonal variations in the pattern of LH secretion (Lincoln, 1979). Whilst there is general agreement that underfeeding in males reduces LH secretion, the involvement of this hormone in facilitating nutrition-induced increases in testis size remains controversial.

In mature rams, diets which were formulated to provide either 50% above or 25% below maintenance requirements in protein (5.5% digestible crude protein) but equivalent levels of energy (7.2 MJ DE/d), had no effect on testis size but the rams fed the 'low' protein diet had significantly fewer LH pulses than those on the 'high' protein diet (Lindsay *et al*, 1984). Similarly, a significant decrease in LH pulses was also observed in rams fed a low energy ration compared with those on a maintenance diet (Martin *et al*, 1989). In 13-month-old Creole bulls fed either a high or a low concentrate ration, which supported mean daily growth rates of 780 and 370 g, respectively (Gauthier and Berbigier, 1982), the lower ration resul-

ted in reduced mean plasma LH and testosterone concentrations. This effect appeared to be due to a significant reduction in the number of pulses of these hormones per d (LH: 2.55 vs 0.63; T: 2.50 vs 0.75 pulses per d, $P < 0.05$), without there being any alteration in their basal levels. Thus the reduced LH pulsatility in the underfed animals may have resulted from an effect of the diet on either the hypothalamic 'pulse generator' or on the sensitivity of the pituitary to GnRH stimulation. However, the finding that the secretory LH response of the pituitary to an injection of synthetic LHRH was greater in underfed animals than in those fed control diets (Campbell *et al*, 1977; Beal *et al*, 1978; Gauthier and Berbigier, 1982) suggests that the reduction in LH pulsatility observed in the slower growing underfed animals may be due primarily to a decrease in release of hypothalamic hormones that control anterior pituitary function (Campbell *et al*, 1977; Gauthier and Berbigier, 1982). Such a circumstance may also have the effect of reducing the pituitary stores of LH, which was reported to occur in rams maintained on a low energy diet (Alkass *et al*, 1982), though interestingly, there was no concomitant decrease in pituitary FSH content. In contrast, in male rats, underfeeding for 10–20 d resulted in an increase in pituitary concentration of LH, but not FSH, which suggested that in this species, underfeeding impaired release mechanisms for LH (see above, decrease in GnRH pulsatility) rather than factors controlling hormone synthesis (Howland, 1975).

To elucidate the physiological mechanism(s) mediating such endocrine responses during undernutrition, Gauthier and Coulaud (1986) studied LH pulsatility in adult bulls fed high and low planes of nutrition, before and after castration and after replacement therapy with testosterone in the castrates. They found that after castration, there was a marked increase in LH pulsatility in both groups and that the previous inhi-

bition of LH pulsatility, induced by undernutrition, disappeared. After treatment with 30 mg testosterone per d for 2 weeks, which produced the same plasma levels of this hormone in the 2 groups, marked suppression of LH pulsatility in the underfed animals was reimposed. A similar finding has been reported in rams (Tjondronegoro *et al*, 1991), in which the effects of both testosterone and bovine follicular fluid were studied after castration. Accordingly, it appears that the effects of undernutrition on gonadotrophin released may be mediated by hypersensitivity of the hypothalamo-pituitary axis to testosterone. Presumably therefore, even the reduced testosterone concentrations that occur as a result of underfeeding are sufficient to exert this endocrine effect.

The increase in testis size in bulls (Nolan *et al*, 1990) and rams (Ritar *et al*, 1984; Martin *et al*, 1987) resulting from feeding high energy diets (including diets supplemented with 750 g lupin grain) is not accompanied by a sustainable elevation in either pulsatility or mean concentration of LH. However, when rams were fed much larger amounts of lupin grain or cowpeas (2% of body weight) for 77 d, plasma LH concentrations were significantly elevated compared with that in hay-fed controls (Pomares *et al*, 1991). Martin *et al* (1990) reported that in rams fed a sub-maintenance diet for 2 months (sufficient to reduce LH secretion during that period) and subsequently fed an extra ration which included 750 g of lupin grain/d, plasma LH concentrations were significantly elevated 2 d after commencement of the extra ration. However, it is possible that this increase in LH was merely a 'rebound' response which can occur following temporary suppression of hormones; such a response was reported for both LH and FSH in rams after temporary suppression of these hormones by treatment with epidermal growth factor (Brown *et al*, 1989). It also appears that glucose is not directly involved in gona-

dotrophin release, since infusions of 1.4 M glucose solutions in rams for 11 d failed to increase either LH or FSH (Boukhliq *et al*, 1991).

It appears that nutrition-induced increases in testicular size is associated with either an increase in the size and length of the seminiferous tubules (Oldham *et al*, 1978) or an increase in the number of expanded tubules (Nolan *et al*, 1990). These effects presumably occur as a result of more spermatogenic cells and an increase in testicular fluid secreted by the Sertoli cells in response to FSH and testosterone (Vitale *et al*, 1973; Courot and Ortavant, 1981). Though FSH concentrations were not measured in these studies, the increase in seminiferous tubule size may indicate a differential effect of nutrition on gonadotrophin release. Indeed, in rams fed 750 g of lupins/d in addition to a maintenance diet (Tjondronegoro *et al*, 1990), mean plasma FSH concentrations were significantly elevated compared with those in control animals on the maintenance diet or other rams on half maintenance. The increased values were in evidence after the fifth day of feeding and remained elevated for at least 28 d. Interestingly, FSH concentrations did not differ materially between the controls rams or those on the half maintenance diet (Tjondronegoro *et al*, 1990), a result which is in accord with earlier findings that showed there was no significant depletion in pituitary FSH content in rams fed low energy rations (Alkass *et al*, 1982). In Merino ram lambs supplemented with lupin grain from birth (through feeding the dams 500 g/ewe/d until weaning at 12 weeks of age) to puberty (10 g/kg body weight/d from weaning until 28–30 weeks of age), a more sustainable increase in FSH plasma concentrations occurred (Brown, 1993). The mean levels of this hormone peaked about 10–20 d earlier (31–40 d of age) than that in the control lambs (51–60 d of age) and remained at an elevated level for 10–20 d longer (until

71–80 d of age) before the decline to low levels (Brown, 1993). Furthermore, mean plasma FSH concentrations remained at a significantly ($P < 0.05$) greater level in these animals than in the controls for the 14 months duration of the experiment (Brown, unpublished data).

In monogastric animals, which are more dependent upon dietary protein as a source of nitrogen than ruminants, protein-calorie deficient diets produce very marked morphological changes in the anterior pituitary (Godwin and Platt, 1960; Dickerson *et al*, 1964; Platt and Stewart, 1967), which were consistent with there being a reduced storage of, but not necessarily a complete absence of, trophic hormones in this gland.

Androgens

Before the advent of routine plasma testosterone assays, the weight of the reproductive accessory glands and/or the concentrations of their secretion of fructose and citric acid (which are known to be androgen dependent) were the criteria by which androgenic activity was assessed (Mann and Lutwak-Mann, 1951; Mann and Walton, 1953). From studies of the fructose and citric acid content of semen obtained from young bulls (Davies *et al*, 1957; Mann *et al*, 1967; Baranos *et al*, 1969), it was postulated that restricted feed intake markedly delayed the onset of testosterone production, which preceded the delay in spermatogenesis. This notion was given greater credence with the advent of testosterone assays, when Mann *et al* (1967) showed that the testes of undernourished young bulls contained and secreted less testosterone and had a lower testosterone/androstenedione ratio than those in normal-fed control twins. The larger amounts of androstenedione in the undernourished animals appeared to be associated with altered activity of the enzyme

(17 β -hydroxysteroid dehydrogenase) involved in steroid biosynthesis (Mann *et al*, 1967).

Restricted feeding of mature bulls over a period of 23 weeks also resulted in marked depression of fructose and citric acid concentrations in the semen (Mann and Walton, 1953). Because, in these animals, seminal characteristics were unaffected by the treatment, it was concluded that spermatogenesis may either proceed at a lower level of testosterone production than that required for accessory gland function, or that the testes have a greater propensity for obtaining testosterone from the blood than do the accessory glands (Mann and Walton, 1953). However, later studies have shown that testosterone is present in testicular lymph (Lindner, 1963) and rete testis fluid (Voglmayr *et al*, 1966; Cooper and Waites, 1974; Amann and Ganjam, 1976), whilst androgen binding protein (ABP) occurs in rete testis fluid and seminal plasma (Jégou *et al*, 1978; Jégou *et al*, 1979) and accordingly, may indicate existence of extra vascular mechanisms for 'intra-gonadal' transport of androgens, whereby Leydig cell secretions can exert an influence on tubular function.

In adult Merino rams, in which restricted food intake for 3 months resulted in a reduction of body fat to less than 12% of live-weight (25–49% for well-fed animals), mean testosterone output was also considerably reduced ($0.4 \pm \text{sem } 0.2$ mg/d) when compared with that (3.5 ± 0.7 mg/d) for well-fed control rams (Setchell *et al*, 1965). This is in accord with the finding that reduced energy intake in rams resulted in a decrease in the fructose content of ejaculates (Moule *et al*, 1966), indicating that androgenic activity was suppressed. Setchell *et al* (1965) reported that the reduced testis weight in the underfed animals was accompanied by a decrease in testicular blood flow, oxygen uptake and glucose uptake. These changes in particular indicate that metabolic activity

of the testis is also lowered during undernutrition, though the fraction of the oxygen uptake derived from oxidation of glucose was unchanged (Setchell *et al*, 1965). The lack of any effect of undernutrition on peripheral plasma testosterone levels in the mature Merino rams studied by Parr and Tilbrook (1990) was possibly due to the very short period of restricted feeding (10 d) which was effective in causing only a modest loss in body weight (5.9%), much of which may be due to loss of gut-fill of water.

As alluded to earlier, increasing the dietary energy intake in young bulls (Reeves and Johnson, 1976; Nolan *et al*, 1990) was associated with an increase in testicular size and an elevation in both plasma and testicular testosterone concentrations, without there being any significant change in mean or basal plasma LH concentrations, or in LH pulse height frequency or amplitude (Nolan *et al*, 1990). Moreover, the increased energy intake also resulted in an enlargement of the Leydig cells and such growth may constitute an increase in the amount of smooth endoplasmic reticulum, thereby facilitating the observed rise in testosterone synthesis (Zirkin *et al*, 1980; Nolan *et al*, 1990). These findings imply that, in the growing bull at least, additional nutrient intake may alter Leydig cell function directly, perhaps by affecting sensitivity to gonadotrophic stimulation. In contrast, a high protein lupin grain supplement fed to Booroola and control Merino rams for 9–15 weeks produced no significant effect on the tonic secretion of either testosterone (Ritar *et al*, 1984; Martin *et al*, 1987) or LH (Sutherland and Martin, 1980; Ritar *et al*, 1984; Martin *et al*, 1987). This finding is surprising in view of the fact that there was an increase in testis size in the supplemented rams. Martin *loc cit* concluded that the resulting enlargement of the testes did not appear to involve an increase in the responsiveness of the testis of LH. Presumably, the increase in testis

size in these rams was associated with an increase in the volume of the seminiferous tubules (Oldham *et al*, 1978). The lack of an increase in testosterone concentrations may be due to the inability of this diet to affect Leydig cell function directly.

THE IMPORTANCE OF AMINO ACIDS FOR REPRODUCTIVE FUNCTION IN MALES

In ruminants, provided that metabolisable energy is not limiting, degradation of dietary protein by the rumen microorganisms provides the animal with a reasonably constant amino-acid supply (Reid, 1990), which in general, is sufficient to meet requirements for maintenance, slow growth or early pregnancy (Lloyd Davies, 1982). Additional, essential amino acids that are required to facilitate fast growth, are provided directly to the animal through the post-ruminal digestion of undegraded protein. Although certain amino acids appear to be necessary for the process of spermatogenesis (Hopwood and Gassner, 1962; Setchell *et al*, 1967), the grazing ruminant would not normally encounter deficiencies in these substances unless the pasture is of very low protein content. Furthermore, in adult rams, it appears that the testis is able to utilize glucose to synthesize most of the amino acids that are present in high concentrations in testicular fluid, with the possible exception of glycine (Setchell *et al*, 1967). This may also be the case in bulls, as Oltjen *et al* (1971) concluded from their studies that the young bull is capable of synthesizing all of the essential and non-essential amino acids needed for fertility, even when fed a protein-free diet in which urea served as the sole source of dietary nitrogen. On the other hand, monogastric animals, such as pigs, are extremely dependent upon dietary protein as a source of amino acids but as these animals are intensively raised and there-

fore mostly hand fed with proprietary feed mixtures, protein deficiency should not occur.

The early work of Courier and Raynaud (1932), Cunningham and Hopkirk (1935) and Cunningham *et al* (1937), which showed that rats fed a diet deficient in lysine had poorly developed testes, provided some of the first evidence that specific amino acids may be of importance for normal reproduction in males. From later work in rats, it was concluded that whilst leucine, methionine or valine did not appear to be essential for testicular function, lysine, tryptophane, phenylalanine, arginine and histidine were crucial and their absence resulted in moderate to marked histological and cytological changes in the testes and impairment of spermatogenesis (Maun *et al*, 1945, 1946a, 1946b; Samuels, 1950; Shettles, 1960). In boars, tryptophane deficiency also resulted in testicular atrophy, marked disorganization of the testes and the absence of spermatogenesis (Shettles, 1960), whilst increasing the amounts of lysine (Stepurin and Miruskina, 1969; Netesa and Pashkevich, 1971) or methionine (Tommé and Loskutnikov, 1972) in diets fed to boars, improved the quality and the quantity of their semen. In young bulls nearing puberty, the blood plasma content of most of the free amino acids was reduced as a result of undernutrition (Baronos *et al*, 1969) or feeding a purified diet containing urea as the sole source of dietary nitrogen (Oltjen *et al*, 1971). In the latter case, however, the amino-acid content of the seminal plasma seemed little affected by the diet and may indicate a preferential need for the available amino acids to support fertility over growth. It would appear therefore that young bulls are capable of synthesizing all of the essential and non-essential amino acids needed for fertility even when fed a protein-free (urea-containing) diet (Oltjen *et al*, 1971).

It is not clear how specific amino acids actually induce these reproductive effects

but the mechanism may involve the hypothalamic neurones rather than any direct effect on the testis. In rats, monkeys and sheep, *in vivo* administration of agonists of the neuroexcitatory amino acids glutamate and aspartate induced the release of LH (Wilson and Knobil, 1982; Gay and Plant, 1987; Ebling *et al*, 1989; Estienne *et al*, 1990; Jansen *et al*, 1991), an effect which was evidently mediated by these substances triggering GnRH release (Bourguignon *et al*, 1989; Claypool and Terasawa, 1989). Moreover, it has been shown that antagonists of neuroexcitatory amino acids can inhibit the release of GnRH from the hypothalamus (Bourguignon *et al*, 1989) and suppress LH release (Arslan *et al*, 1988), while pre-treatment of monkeys with a GnRH receptor antagonist eliminated the ability of *N*-methyl-D, L-aspartate to stimulate LH release (Gay and Plant, 1987).

THE EFFECTS OF PLANT OESTROGENS ON REPRODUCTIVE PERFORMANCE IN MALES

The adverse effects that grazing 'oestrogenic' pastures has on reproduction in ewes is well known (see reviews by Moule, 1961; Moule *et al*, 1963). Bennetts *et al* (1946) claimed that the ingestion of oestrogenic pasture by flock rams did not lower their fertility. However, the findings of Moule and Mattner (1961) suggested that spermatogenesis in rams could be depressed by intramuscular injections comprising the equivalent of 25 µg stilboestrol dipropionate per ram per d over 6 weeks. Such a treatment resulted in a decrease in the total number of spermatozoa in ejaculates, the motility of spermatozoa and the percentage of live and morphologically normal spermatozoa, from 5 weeks after commencement of treatment. These effects were not long lasting, for the animals showed substantial recovery in the seminal characteristics within 6 weeks of

ceasing treatment. The oestrogen equivalent of 25 μg stilboestrol used in this study exceeded the minimum oestrogen intake known to adversely affect the breeding performance of ewes (Moule, 1961) but may be within the range of normal oestrogen intakes for some animals grazing oestrogenic pastures.

Nevertheless, the above effects induced by stilboestrol treatment were not in evidence in Merino rams grazed on red-clover-dominant pasture from weaning for a period of 12 months (George and Turnbull, 1966). In these animals, puberty was not retarded, nor did the red clover have any detrimental affect on liveweight, weight of testes and epididymides or on the number of epididymal sperm when compared with control rams grazing grass-dominant pasture. In this study, it was estimated that the effective intake of oestrogenic substances obtained from grazing the red-clover pasture was greater than the equivalent of 15 μg stilboestrol dipropionate per d (George and Turnbull, 1966).

With the huge amount of oestrogen that is required to produce seminal degeneration in bulls, it is unlikely that they could consume sufficient oestrogenic pasture to affect spermatogenesis (Moule and Mattner, 1961) and the evidence available indicates that cattle are unaffected by grazing oestrogenic pastures that are detrimental to reproduction in sheep (Bennetts *et al*, 1946).

CONCLUDING REMARKS

There seems to be little doubt that reproductive function in the young animal is more susceptible to changes in dietary energy or protein than in the adult. From early in life, reduction of these components of the diet to levels below that required to support normal body growth, can produce detrimental effects on reproductive development and under conditions of severe feed restriction,

such effects may result in long-term damage to gonadal and neural tissues. In this regard, young boars appear to be more vulnerable than their ruminant counterparts and this is probably due in part to their total dependence on dietary protein as a source of nitrogen.

Restricted energy intake in adult boars, bulls and rams appears to have more of an adverse effect on accessory gland function, and therefore on androgen activity, than on spermatogenesis, whilst protein deficiency generally reduces accessory gland secretions and semen quality. However, these physiological and endocrine changes appear to be temporary, as re-feeding previously underfed adult animals unusually restores normal reproductive function. Sexual activity may be suppressed by low energy intake but the reduced levels of libido in underfed bulls and rams seems to be more a consequence of reduced physical strength, than an effect on neural centres controlling sexual activity. In general, high energy intake has beneficial effects such as advancement of onset of puberty as a result of enhanced reproductive development and increased testicular size and sperm production in both young and adult animals, whilst excessive intake can have detrimental effects on reproduction.

There is now considerable evidence suggesting that the influence of nutrition on reproductive processes are mediated *via* effects of dietary constituents on the hypothalamic-pituitary axis, although there is some indication that dietary changes may affect the testis directly. That some nutritional regimes imposed on animals can alter the volume of ejaculates and androgen activity without necessarily affecting spermatogenesis, suggests that certain constituents of the diet can differentially affect the production and/or release of LH and FSH. The findings that severe protein deficiency produces detrimental effects on semen quality may implicate certain amino acids in mecha-

nisms controlling stimulation of FSH secretion. Indeed, studies on agonists and antagonists of neuroexcitatory amino acids have demonstrated an important role played by certain of these compounds in secretion of hypothalamic-releasing factors. FSH by binding to Sertoli cells appears to stimulate the synthesis of many proteins (Sharpe, 1984) including inhibin and ABP. The major role of ABP is uncertain but it has been suggested that it is involved in transport of androgens within the testis and concentrates them at sites that facilitate spermatogenesis (Martin *et al*, 1990), or that it mediates the action of gonadotrophins on Sertoli cells to enhance and promote spermatogenesis (Courot and Ortavant, 1981). However, as control of FSH secretion also involves inhibin, a study of the influence of dietary constituents on Sertoli cell function in relation to inhibin and ABP production and on the responsiveness of the pituitary to inhibin, is also needed.

Attempts to elucidate the mechanism(s) by which energy intake influences testicular size and function have produced conflicting findings. Possibly this is partly due to the fact that many feeding regimes designed to produce high or low energy intakes have necessarily resulted in alteration of the protein content. Whilst it seems certain that undernutrition in animals leads to a decrease in androgen secretion and activity as a result of decreased LH release, there is convincing evidence to show that high energy diets promote increased androgen secretion (principally testosterone) in the absence of a concomitant sustainable increase in LH secretion. This suggests that high energy diets may act at the level of the testis directly by altering the size and/or function of the Leydig cell. The possibility exists that high energy intake may influence enzyme activity involved in the conversion of androstenedione to testosterone, or it may alter the Leydig cell content of smooth endoplasmic reticulum, the amount of which is highly cor-

related with the total amount of testosterone produced. However, there is also some evidence to suggest that high energy intake facilitates increases in FSH secretion, which may explain the beneficial effects of such diets on spermatogenesis and sperm production. This aspect may be of particular relevance in young animals, since a rise in FSH secretion occurs concomitantly with an increase in the number of Sertoli cells during early life. Accordingly, enhancement of FSH secretion during this period may therefore permit a sustainable increase in sperm production and improve semen quality later in life, which could have the effect of reducing the huge variation in sperm production that normally occurs between potential sires.

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