The effect of escape protein and carbohydrate source on performance, metabolism and wool production of ewes during mid-gestation
by Robert Francis Padula

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University

Abstract:
The objective of this experiment was to evaluate the influence of diets differing in quantity of escape protein (EP) and energy (carbohydrate; CHO) source on metabolism of Targhee ewes during mid-gestation. Ewes were allocated by randomization to one of six treatment (TRT) groups utilizing a 2 x 3 factorial arrangement that included either urea (U), soybean meal (SBM) or blood meal (BM), and starch (STAR) or cellulose (CELL). Trial duration was 63 d with two experimental periods. Ewes fed BM gained more ($P < .10$) weight during the experiment than those fed LI or SBM. A significant protein by energy interaction was detected with U-CELL ewes gaining less ($P < .05$) total weight than the other treatment combinations. BM ewes had greater ($P < .05$) albumin (ALB) concentrations than U and SBM during period 1 or U in period 2. Total protein (TP) concentrations tended to be higher ($P > .10$) for BM than U or SBM with no differences ($P > .10$) for blood urea N (BUN) between TRT. Higher TP and ALB and similar BUN concentrations for BM may be indicative of increased amino acid absorption from the gut and efficient utilization of them by the liver. Lambs born to BM ewes had greater ($P < .05$) 90 d weights than U or SBM lambs. Energy source had no influence ($P > .10$) on ewe weight change. Ewes fed CELL had lower ($P < .05$) TP and BUN concentrations in period 1 and BUN in period 2 than STAR ewes. This is related to lower microbial protein production and less EP reaching the small intestine for CELL compared to STAR. Ewes fed CELL in period 2 retained less ($P < .05$) dietary N than STAR ewes. Ewes fed EP had blood metabolite profiles indicative of improved quality and/or quantity of N reaching the small intestine for absorption and metabolism in the liver.

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Robert Francis Padula

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APPROVAL

of a thesis submitted by

Robert Francis Padula

This thesis has been read by each member of the graduate committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

6-29-90 — Date

Veal M. Thorn — Chairperson, Graduate Committee

Approved for the Major Department

7-23-90 — Date

Leonard C. Gaynor — Head, Major Department

Approved for the College of Graduate Studies

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ABSTRACT

The objective of this experiment was to evaluate the influence of diets differing in quantity of escape protein (EP) and energy (carbohydrate; CHO) source on metabolism of Targhee ewes during mid-gestation. Ewes were allocated by randomization to one of six treatment (TRT) groups utilizing a 2 x 3 factorial arrangement that included either urea (U), soybean meal (SBM) or blood meal (BM), and starch (STAR) or cellulose (CELL). Trial duration was 63 d with two experimental periods. Ewes fed BM gained more ($P < .10$) weight during the experiment than those fed U or SBM. A significant protein by energy interaction was detected with U-CELL ewes gaining less ($P < .05$) total weight than the other treatment combinations. BM ewes had greater ($P < .05$) albumin (ALB) concentrations than U and SBM during period 1 or U in period 2. Total protein (TP) concentrations tended to be higher ($P > .10$) for BM than U or SBM with no differences ($P > .10$) for blood urea N (BUN) between TRT. Higher TP and ALB and similar BUN concentrations for BM may be indicative of increased amino acid absorption from the gut and efficient utilization of them by the liver. Lambs born to BM ewes had greater ($P < .05$) 90 d weights than U or SBM lambs. Energy source had no influence ($P > .10$) on ewe weight change. Ewes fed CELL had lower ($P < .05$) TP and BUN concentrations in period 1 and BUN in period 2 than STAR ewes. This is related to lower microbial protein production and less EP reaching the small intestine for CELL compared to STAR. Ewes fed CELL in period 2 retained less ($P < .05$) dietary N than STAR ewes. Ewes fed EP had blood metabolite profiles indicative of improved quality and/or quantity of N reaching the small intestine for absorption and metabolism in the liver.

INTRODUCTION

Montana native range provides much of the nutrition for gestating ewes during winter because of the absence of snow cover. Early work by Van Horn et al. (1959b) reported it was profitable to supplement gestating ewes grazing Montana winter range two out of every three years with .15 kg of a cereal-based, 18-20% crude protein supplement. More recently, Harris et al. (1989) reported that pregnant ewes grazing winter range did not receive adequate protein nutrition, and protein appears to be more limiting than energy. However, these studies did not evaluate protein sources not degraded extensively in the rumen (escape protein, EP). Hoaglund et al. (1989) reported that pregnant ewes fed straw diets supplemented with blood meal had improved N balance, ewe weight and body condition score changes, and wool growth in comparison to those fed urea or soybean meal. They speculated that EP reaching the small intestine in blood meal ewes was the primary reason for improved metabolism and performance.

Diets containing starch as the primary carbohydrate (CHO) source provide a readily digestible energy source for microbial protein synthesis (Merchen et al., 1987; Rooke and Armstrong, 1989). Increased microbial protein production should provide additional N in the form of bacterial or

protozoal amino acids for absorption by the small intestine (Stern and Hoover, 1979). Diets high in cellulose provide a lower digestible energy source and may reduce microbial protein synthesis, resulting in an increased demand for amino acids from EP to maintain production (Polan, 1988).

The objective of this study was to evaluate the influence of supplements differing in quantity of EP and CHO source on ewe metabolism and productivity during mid-gestation.

LITERATURE REVIEW

Ewe Nutrient Requirements

Nutrient requirements for livestock have traditionally separated maintenance from production. Maintenance requirements are determined by live weight of the animal and environmental conditions. Production requirements are determined by the amount and nature of production (van Es, 1972).

Maintenance is a relatively constant state in mature animals and can be fed so there is no gain or loss of weight over a period of time (Graham, 1982). An animal's energy requirement for maintenance is the amount of energy the animal must consume to neither gain nor lose weight. Fasting heat production is used as a baseline in assessing energy requirements independent of the diet fed. The net energy required for maintenance (NE_m) is the daily quantity of energy resulting in a zero change in body energy (NRC, 1985a). The requirement for maintenance is not static. Animal weight, activity and thermal homeostasis all affect NE_m (Graham, 1982).

Heat losses due to shearing will increase NE_m, as wool is a very effective insulator. At a given feeding level, the shorter the fleece the higher the lower critical temperature (LCT) of the sheep (Graham, 1982). Shearing will increase NE_m if environmental temperature is below the LCT (NRC, 1985a).

Van Es (1972) and NRC (1985a) did not mention a specific energy requirement for wool growth. NRC (1985a) stated the energy requirement for wool production represents a small fraction of the total energy consumed. Graham (1982) contended that the efficiency of energy utilization for wool growth is not known and protein rather than energy supply determines wool growth rate.

The most common method for reporting protein requirements is based on the concentration of protein as a percentage of dry matter in terms of biological value (Ørskov, 1982; NRC, 1985b). For absolute maintenance, tissue protein degradation and synthesis need to take place at equal rates. To define a maintenance protein requirement, one must consider unavoidable-N losses from the body and amount fed to offset these losses.

Unavoidable-N losses occur in the form of metabolic fecal N (MFN), endogenous urinary N (EUN) and excretions from the skin. A comparison of 10 systems for assessing protein requirements for ruminants has been reviewed (NRC, 1985b). Calculation of MFN and EUN is quite variable between systems; however, certain principles are fundamental. MFN is based on the animal's intake feed, while EUN is a function of animal weight.

NRC (1985a) separates skin N losses into dermal loss and loss due to wool growth. Loss of N due to wool growth on maintenance rations may vary at least two-fold depending on genotype and amount of S-amino acids absorbed from the small intestine (Graham, 1982).

The nutrient requirements of the pregnant ewe are higher than maintenance due to the products of conception and mammary gland development. Increase in fetal weight during early pregnancy is small, with the majority of fetal growth (approximately 70%) occurring during the last four weeks of gestation (NRC, 1985a). During early gestation, most research has focused on the degree of nutrient restriction that can be applied before embryo and fetal survival is affected. Blockey et al. (1974) concluded that fasting for 3 d from either day 1, 5, 8, 10 or 12 after mating has no adverse effect on fertility in twin-ovulating ewes.

During the third and fourth weeks of gestation (implantation stage), there is a strengthening of the bond between the embryo cotyledons and the maternal caruncles. Many of the nutritionally induced deaths occurring between days 15 and 30 after mating arise from undernutrition following mating (Robinson, 1983). McDonald et al. (1981) reported that death of one or more embryo during the third and fourth weeks of gestation tends to disturb the balance in the distribution of fetuses in the uterine horns. This imbalance results in inability of the surviving embryos to utilize the vacated maternal cotyledons (Robinson, 1983). This results in a higher proportion of ewes rebreeding at more than 19 days after a fertile mating, reduced lambing percentage, and smaller lambs at birth.

Research by Doney and Gunn (1981) indicated that changes in nutritional levels post-mating, either up or down, may induce greater ova losses than

nutritional levels held constant at an intermediate level. Thomas et al. (1989) reported a lower percentage of lambs born per ewe exposed for range ewes supplemented on alternate days compared to ewes supplemented on a daily basis. They speculated that an abrupt change in nutrient intake from breeding to a lower plane of nutrition on winter range and lack of a constant nutrient supply to those supplemented on alternate days may have predisposed them to more reproductive wastage.

Robinson (1982) indicated fetal losses due to a low plane of nutrition are more prevalent in young ewes or those in poor condition at mating. Embryonic mortality is also increased as ovulation rate increases.

Earlier research by El-Shiek et al. (1955) and Foote et al. (1959) demonstrated increases in embryonic mortality when ewes were overfed during early gestation. More recently, Parr et al. (1987) conducted a study in which Merino ewes were fed at 25%, 100% and 200% maintenance on days 2 to 14 post-mating. They reported a significant reduction ($P < .05$) in pregnancy rate (48% vs. 68%; 68% vs. 67%) for ewes fed at the high level when compared to those fed at a medium or low level. A decline in peripheral progesterone concentration with increasing nutrition was reported. They concluded that effect of nutrition on plasma progesterone concentrations may be due to a higher clearance rate of progesterone since blood flow to the liver increases with feeding and the liver is a major site of progesterone catabolism. If the ovary does not compensate for this increase in catabolism,

progesterone concentrations could fall below the threshold necessary for embryo survival.

The placenta and fluids (allantoic and amniotic) are also products of conception that increase the ewe's nutritional requirement. Placental weight appears to plateau at about day 100. Severe undernutrition during the first 100 d can reduce the number of cotyledons and total weight of cotyledonary tissue (Robinson, 1977). Faichney and White (1987) reported moderate dietary restrictions resulted in increased placental size from day 50, even when imposed after day 100.

Both allantoic and amniotic fluid increase rapidly in early pregnancy, followed by a leveling off in mid-gestation (Robinson, 1982). Urine formed in the mesonephros of the fetal lamb passes into the allantoic cavity until about day 90 of gestation. Thereafter, urine passes in increasing quantities into the amniotic sac due to occlusion of the urachus and patency of the urethra (Hafez, 1987). As fetal growth and metabolism increase as gestation progresses, a second increase in fluid volume is observed. During late gestation, daily gains in fetal fluids of 250 $g*d^{-1}$ have been observed in quadruplet-bearing ewes (Robinson, 1982).

Absolute growth rates of the fetus place virtually no additional requirements on the ewe during the first month of gestation. Fetal weights (Joulbert, 1956) at 25 and 40 days are approximately .3 and 5 g, respectively. Hulet et al. (1969) offered ewes either 75% or 150% of their estimated maintenance

energy requirements from mating until day 21 or 30, without affecting fetal weight. Similar results were reported earlier by Foote et al. (1959), El-Shiek et al. (1955) and Wallace (1948).

Requirements listed in NRC's (1985a) "Nutrient Requirements of Sheep" for ewes during the first 15 to 17 weeks of gestation are intended to provide for maintenance, wool growth and small (30 g) daily gains. Wallace (1948) indicated fetal weight was not affected by ewe weight decreases of up to 7% of body weight. Russel et al. (1977) suggested that unless undernutrition in mid-gestation was severe, mature ewes would compensate for inadequate nutrition during late gestation. However, inadequate nutrition during mid-gestation in the young primiparous ewe did have a significant effect on fetal weights. Chestnutt (1989) concluded that high quality silage fed during mid-gestation only improved levels of body reserves, with little effect on fetal weight. In addition, he found that feeding high quality silage during mid-gestation appeared to reduce intake during the last week of gestation.

Ewe nutrient requirements increase in late gestation due to increased demands for fetal growth and udder development. Results of undernutrition during late gestation include impaired milk production capability, reduced mothering instinct and lower birth weights leading to reduced lamb viability (NRC, 1985a). Faichney and White (1987) compared fetal growth of ewes on a maintenance ration (M) to those subjected to moderate dietary restriction from days 50 to 100 (RM), days 100 to 135 (MR), or days 50 to 135 (RR). RR

fetuses were smaller, RM fetuses larger, with MR fetuses unaffected compared to those of ewes fed M.

Mellor and Matheson (1979) indicated that sustained severe undernutrition for three to four weeks in late gestation progressively decreased fetal growth rate. Abrupt severe undernutrition during late gestation can slow down or in some instances reduce fetal growth by 50% within three days. However, even when cessation of fetal growth was maintained for one week, growth rates returned to normal when ewes were reintroduced to a high plane of feeding.

Sykes and Field (1972) reported undernutrition of ewes in late gestation causing a 25% decrease in lamb birth weight had no detrimental effect on the fetus. This is in support of Robinson (1977) who indicated the undernourished lamb at birth appears malproportioned in relationship to a well fed lamb simply because it is lighter and at an earlier stage of differential growth and development.

Rattray (1974) presented estimates for metabolizable energy (ME) requirements for gestating ewes with a breeding weight of 55 kg according to stage of gestation and fetal number (Table 1). These values demonstrate the influence of stage of gestation and fetal number on nutrient requirements. Meeting the nutritional requirement (particularly towards the end of gestation and with multiple fetuses) can be both difficult and uneconomical.

Table 1. Multiple of maintenance requirements for gestating ewes based on stage of gestation and fetal number.[a]

Gestation (d)	Single	Twin	Triplet
100	1.2	1.5	1.6
120	1.4	1.9	2.1
140	2.0	2.6	2.8

[a]Values based on total birth weight of 4.9, 7.9 and 9.1 Kg for single, twin and triplet lambs, respectively.

Publications on nutrient requirements for sheep (ARC, 1980; NRC, 1985a) recommend the utilization of body reserves when energy requirements of the prolific ewe exceed those supplied by voluntary intake of high quality diets.

Jordan and Hanke (1988) fed ewes above (32%) or below (10%) the NRC recommended total digestible nutrient (TDN) requirements for early and late gestation (1.8 and 2.8 lb TDN, respectively) during the last 90 d of gestation. Ewes were in above average body condition at time of breeding (3.9 score on a scale of 1=thin to 5=fat). All ewes, regardless of energy level, gained weight and improved in body condition score. Ewes fed at the higher intake level gained more ($P < .05$) weight, but no significant differences were detected in lamb birth weight. They concluded fat reserves minimized the effects of inadequate energy intakes during gestation.

Rumen Microorganisms

Much of the current information regarding the predominant bacteria in the rumen deals with a population that is free or detached from plant material.

However, microscopic studies indicate a second population is firmly attached to and within feed particles (Van Soest, 1982). A third group attached to the epithelial cells of the reticulo-rumen mucosa is also present. More than 200 species and strains of microorganisms have been isolated from the rumen (Baldwin and Allison, 1983). Hungate (1966) classified ruminal microbes according to type of substrate they attack in the rumen. They were: cellulolytic, hemicellulolytic, amylolytic, fermentors of sugars, bacteria utilizing acids, methanogenic, proteolytic and lipolytic.

Baldwin and Allison (1983) generalized that cellulolytic bacteria do not ferment monosaccharides and are restricted to di- and trisaccharides and oligosaccharides released during the hydrolysis of cellulose as carbon and energy sources. A number of cellulolytic bacteria are also amylolytic, utilizing starch as an energy source (Hungate, 1966). Baldwin and Allison (1983) reported that starch digesting bacteria vary in numbers due to variation in starch content of diets. They also indicated bacteria utilizing soluble sugars as energy sources are also present, with their population dependent on dietary sugar content.

Hemicellulose constitutes a large percentage of forage consumed by ruminants (Van Soest, 1982). The ability to digest hemicellulose is characteristic of all cellulolytic strains, with hemicellulose being digested to about the same extent as cellulose (Hungate, 1966).

All rumen bacteria which digest polysaccharides are capable of utilizing mono- or disaccharides (Hungate, 1966) and play a role in fermenting simple sugars. Simple sugars are available for a short duration after food is ingested; therefore, bacterial species which solely utilize simple sugars are handicapped with cellulolytic and hemicellulolytic bacteria having an advantage compared to bacteria capable of utilizing polysaccharides (Hungate, 1966).

Hungate (1966) identified bacteria with the capability of utilizing acids in the rumen. He reported both succinate and formate are produced by many rumen bacteria, with unknown bacteria having the ability to decompose these acids since they do not accumulate in the rumen. Methanogenic bacteria have been the most difficult to isolate due to their sensitivity to oxygen (Hungate, 1966). Fortunately, methanogenic bacteria are low in numbers (Hungate, 1966), since conversion of valuable substrate to methane and carbon dioxide would seriously deplete the quantity of fermentable product oxidized by the host animal.

Van Soest (1982) indicated some bacterial strains are limited in their spectrum of energy sources, others are more versatile, and much overlapping of bacterial function exists. Baldwin and Allison (1983) noted often times bacteria are dependent upon other species for supplying nutrients.

Ogimoto and Imai (1981) noted rumen protozoa were discovered in 1843, and that many taxonomical, morphological and nutritional investigations have

been conducted. However, understanding of their role and significance is still unclear (Van Soest, 1982). Partial uncertainty arises because in the defaunated animal, the role of protozoa is mainly taken over by bacteria (Lindsay and Hogan, 1972).

Russell and Hespell (1981) reported some protozoa prefer soluble carbohydrates whereas others engulf particulate carbohydrates. Engulfed bacterial cells can serve as the major N source for most species, but particulate proteins, amino acids, peptides and ammonia are also utilized depending on the particular species.

Ruminal protozoa are fermentative aneorobes, and their fermentation products include acetate, butyrate, lactate, carbon dioxide, and hydrogen (Russell and Hespell, 1981). In addition to volatile fatty acid production, protozoa aid in sequestering carbohydrates from rapid bacterial attack; without this a significant portion of the carbohydrate would be fermented to lactate and lower ruminal pH, both of which hinder overall rumen function. An analogous situation also occurs with particulate proteins, whereby engulfment allows for extended proteolysis, slower release of products, and less catabolism of amino acids/peptides to volatile fatty acids (Russell and Hespell, 1981). The extent of protozoal engulfment of rumen bacteria depends on species and bacteria density. Depending on engulfment rate and protozoa concentration, Russell and Hespell (1981) indicated between 2.4 and 45 g bacteria could be digested protozoally per day in a sheep's rumen.

Meyer et al. (1986) reported rumen protozoa numbers, flow of NAN and amino acids increased with increasing amounts of corn in the diet. Also, more feed and endogenous NAN reached the duodenum with increased corn intake. Hino and Russell (1987) reported incubations containing bacteria and protozoa resulted in synergistic increases in ammonia and decreases in nonammonia-nonprotein N, when compared to incubations of bacteria or protozoa alone. They concluded soluble proteins were primarily degraded by bacteria whereas protozoa contribute to the degradation of insoluble proteins.

Ffoulkes and Leng (1988) reported presence of a large population of protozoa in the rumen decreases the amount of microbial and dietary protein that becomes available for digestion in the small intestine. In addition, they indicated protozoa are likely to decrease the efficiency of net microbial growth since they utilize nutrients that are potentially available to the host animal and increase the VFA:amino acid ratios that are absorbed. Volatile fatty acid proportions are often changed by the presence or absence of protozoa. The molar proportion of acetate is less affected than either propionate or butyrate, but has a tendency to be slightly lower in the rumen of ciliate-free animals (Veira, 1986). The implications of VFA proportion shift associated with the presence or absence of protozoa are of importance to the lactating animal. Whitelaw et al. (1984b) reported defaunation resulted in a doubling of the proportion of propionate, methane production was decreased by 50%, and the metabolizability of gross energy increased by 5%. Shifts to lower molar

proportions of acetate and butyrate through defaunation of lactating cows have resulted in depressions of milk fat (Chalupa et al., 1967).

Veira et al. (1983) reported protozoal protein is not a large component of ruminal outflow and supported the observation of Harrison et al. (1979) of preferential retention of protozoa in the rumen. Bird and Leng (1984) reported that increased wool growth resulting from defaunation is an indication of increased absorption of sulfur amino acids.

There is evidence that protozoa are at least a nitrogen source having better amino acid balance than bacteria for host animal nutrition (Hungate, 1978). Also present in the rumen are anaerobic fungi (Bauchop, 1979) and bacteriophages (Ogimoto and Imai, 1981); however, the net contribution of these microorganisms to overall rumen fermentation is not known.

Microbial Protein Synthesis

Various techniques have been used to estimate the amount of microbial digesta leaving the ruminant stomach. Digesta entering the duodenum of ruminants is composed of material of feed, microbial and endogenous origins. Contribution of any one component can be estimated by measuring the concentration of a marker in whole digesta which is specific to and of known concentration in the component (Siddons et al., 1979). The majority of these methods are based on determination of a single chemical marker representing microbial contents.

Diaminopimelic acid (DAPA) was used by Weller et al. (1958) to estimate rate of bacterial protein synthesis. Cell membranes of rumen bacteria contain DAPA, which is absent from plant material (Stern and Hoover, 1979). Stern et al. (1977) indicated that traces of DAPA can be found in protozoa, through protozoal "feeding" upon rumen bacteria.

The DAPA technique involves estimating the ratio of DAPA:N in mixed rumen bacteria in relationship to DAPA in digesta. Ibrahim and Ingralls (1972) used DAPA to measure bacterial protein synthesis and aminoethylphosphoric acid (AEP; found in the lipid fraction of protozoa) to estimate protozoal synthesis. More recently, Whitelaw et al. (1984b) compared DAPA and AEP as markers of microbial protein. They fed three concentrate to forage ratios (50:50, 90:10, 100:0) and found DAPA values of duodenal digesta were similar for all treatments. However, estimates of bacterial N based on DAPA concentrations were highly variable and frequently impossibly high. They reported AEP was also variable, finding no differences between treatments in AEP content of duodenal digesta or protozoal weight (mg/g N). They concluded AEP was an unsuitable marker for rumen protozoa as AEP was also found in rumen bacteria. Both methods (DAPA and AEP) produced variable results, indicating a need for a more reliable marker.

Accuracy of DAPA is dependent upon a constant DAPA:N ratio among rumen microbes or maintaining a constant ratio of microbial species in the rumen (Stern and Hoover, 1979; Whitelaw et al., 1984b). This may explain the

variability among experiments, as it is virtually impossible to maintain constant microbial ratios in the rumen.

Smith and McAllan (1970) used the ratio of ribonucleic acid (RNA) to total N in rumen fluid and rumen microbes to estimate the extent of dietary N converted to bacterial and protozoal N. This technique assumes nearly all dietary RNA is degraded ruminally (Smith and McAllan, 1974) and suggests that microbial protein flow may be overestimated, particularly when protein sources and RNA have been altered to escape ruminal degradation (Buttrey and Cole, 1977). Similar to DAPA, the RNA method is dependent upon uniform bacterial populations, which are altered by diet and rumen environment (Smith and McAllan, 1974).

In comparing DAPA and RNA as microbial markers for microbial N in duodenal digesta, Smith and McAllan (1974) found both methods comparable using a protozoa-free calf. However, using a faunated cow, they found microbial N:non-ammonia N ratios of .78 and .40 for RNA and DAPA methods, respectively. They concluded either considerable amounts of dietary RNA escaped rumen degradation or the DAPA method neglected to account for protozoa. More recently, McAllan and Smith (1984) reported RNA and DAPA techniques for estimating abomasal microbial N flow gave different absolute results but similar relative patterns when different dietary treatments were compared. They attributed these differences to variable composition of the microbial fraction flowing to the omasum.

The benefits and limitations of radioisotopes (^{35}S, ^{15}N and ^{32}P) as tracers to distinguish between microbial and dietary protein have been reviewed by Stern and Hoover (1979). They reported that ^{35}S has been used most frequently. In comparing ^{35}S to DAPA and AEP, Whitelaw et al. (1984b) reported only ^{35}S gave sensible and reproducible results. This is in agreement with Ling and Buttrey (1978) who suggested using ^{35}S where accurate estimates of microbial N are needed; however, the RNA method would be adequate for more general and comparative estimates.

Microbial Yield

The overall concept of microbial maintenance is analogous to maintenance for animals, with growth not occurring until the maintenance requirement is met. Hespell and Bryant (1979) stated maintenance requirement varies according to bacterial species and growth conditions. Early work of Bauchop and Eldsen (1960) compared growth yields of several microorganisms with the theoretical amount of ATP available using g bacterial DM/mole ATP as Y_{ATP}. They suggested Y_{ATP} was relatively constant and proposed a value of 10.5 for rumen bacteria. Hespell and Bryant (1979) suggested theoretical Y_{ATP} yields as high as 26 should be attainable. However, observed yields are generally lower than theoretical (Smith, 1979; NRC, 1985b) with some of the ATP available being used for microbial maintenance (Hespell and Bryant, 1979; Stern and Hoover, 1979).

Changes in cell composition and/or growth media can increase maintenance for cell formation, resulting in decreases in Y_{ATP} from theoretical yields (Hespell and Bryant, 1979). Bacteria usually contain approximately 50% protein, 20% RNA, 3% DNA, 9% lipid and 18% carbohydrate (Nocek and Russell, 1988). Table 2, which was adapted from Hespell and Bryant (1979), demonstrates the change in bacterial composition depending on growth media.

Table 2. Composition of bacteria as affected by growth media (percent dry weight).

Component	Growth Media			
	General	Carbohydrate	Lipid	Protein/Lipid
Protein	47.5	47.5	47.5	65.0
RNA	24.2	8.0	10.0	8.0
DNA	3.4	1.0	1.6	1.0
Lipid	7.0	7.0	25.0	12.0
Carbohydrate	13.5	32.1	11.5	9.6

Nitrogen

Although the major N source for bacterial growth is ammonia, peptides and amino acids are also important (Russell and Hespell, 1981). Nocek and Russell (1988) state ruminal bacteria can incorporate amino acids into microbial protein or ferment them as an energy source giving rise to ammonia. The percentage of microbial nitrogen derived from ruminal ammonia has been reported to range from 40 to 100% (Stern and Hoover,