

# Amino Acid Requirements and Post-Absorptive Metabolism in Cattle: Implications for Ration Formulation

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## Introduction

In addition to decreasing feeding costs, improving the efficiency of utilization of N directly addresses the general concern regarding the environmental footprint of animal production. Excretion of N, especially urinary, may become a potential source of water and air pollution, the latter as N<sub>2</sub>O, a green-house gas, or as small particulate aerosols having a negative effect on air quality [smog; National Research Council (**NRC**), 2003].

It is now acknowledged that improving the formulation of dairy rations requires accurate estimation of both supply and requirements of metabolizable protein (**MP**), far beyond the sole estimation of crude protein (**CP**). A further step involves the transfer of MP supply and requirement into individual essential amino acids (**AA**). Currently, most of the ration balancing models used in North America [e.g. Amino Cow (Evonik AG Industries, Hanau, Germany); Cornell Net Carbohydrate and Protein System (**CNCPS**, Fox et al., 2004) and the CNCPS-derived Agricultural Modeling and Training Systems (**AMTS**); NRC (2001)] have invested considerable time and effort to develop complex rumen sub-models to improve the predictions of the duodenal flow of proteins that will be digested in the small intestine and available to the cow, defined as MP and associated digestible flows of AA. Although fine-tuning of these models might still be needed to improve predictions with variable feed ingredients, their predictions of duodenal flows of proteins or AA fit quite well with measured values (Pacheco et al., 2012). However, the intensive and regular efforts to improve the predictions of supply over the last decades have not been matched by similar efforts to improve the estimations of requirement. Requirements of MP for maintenance in most ration balancing models are still based on work published almost four decades ago (Swanson, 1977) and both requirement for maintenance and milk protein are calculated using a fixed efficiency of utilization, independent of supply. This simplification of the complex biological event of lactation was necessary as a starting point, because “the knowledge of metabolism of nutrients is not as advanced as the prediction of ruminal fermentation, because of the almost infinite metabolic routes connecting various tissue and metabolic compartments, the multiple interactions, and the sophisticated metabolic regulations that determine the partitioning of absorbed nutrients” (Fox and Tedeschi, 2003). The assumed linear relationship between supply and output arising from the use of a fixed efficiency factor is, however, biologically unrealistic. It is well known that MP-allowable milk is usually overestimated at high protein intakes and underestimated at low protein

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intakes with both NRC (2001) and CNCPS (Fox et al., 2004) ration balancing models. The current review proposes updates on the estimation of the requirement of MP and essential AA for maintenance and milk.

## Current Estimations of Requirements

### *Proteins*

This presentation will only deal with requirements for maintenance and lactation, considering mature cows as non-gestating and not changing body weight and composition. Estimation of requirement first requires identification of the proteins and AA that represent a net output, i.e. proteins and AA that will be exported out of the body of the cow. In a second step, the efficiency at which the absorbed protein will be used to support the protein secretion needs to be assigned. Efficiency will be discussed at the end of this section.

Therefore, to begin the first step, definition of the protein required to cover milk protein secretion can be straightforwardly measured as the amount of protein secreted into milk: it currently refers to true protein in NRC (2001) and crude protein in CNCPS (Fox et al., 2004). Unfortunately, the estimation of the protein exported out of the animal to cover requirement for maintenance is not as straightforward as milk protein production. First, the concept of a requirement for maintenance that needs to be fulfilled before milk production occurs does not exist in the lactating dairy cow as the cow will run in negative N balance to support milk production. In addition, estimation of protein requirement for maintenance in the ruminant has always been a challenge due to the inability to feed ruminants a protein-free diet without creating a negative impact on the rumen microflora, a problem exacerbated by the recycling of N into the rumen and associated microbial protein synthesis. In 1977, Swanson made a thorough literature review to estimate “new factors for each of the three loss routes of maintenance nitrogen based only upon appropriate original data from cattle indicative of true maintenance”, these routes being endogenous urinary, scurf and metabolic fecal protein (**MFP**) losses.

Endogenous urinary losses represent the amount of N that would be lost in urine if the animal was consuming a diet adequate in energy but devoid of protein. These losses include creatinine, urea, purine derivatives, nucleic acids, hippuric acid and small quantities of some AA (NRC, 1985). Urinary losses in cattle fed with very low-N diets but adequate energy were used to determine endogenous urinary losses, which were estimated to be  $2.75 \text{ g CP/kg BW}^{0.50}$  per day (with an efficiency of utilisation of 0.67, this translates to a MP requirement of  $4.1 \text{ g CP/kg}^{0.50}$ ). Maintenance requirement for integumental protein include loss and growth of hair, scurf and scales rubbed from the skin surface, along with some N-compounds in skin secretions (Swanson, 1977): requirement were estimated at  $0.2 \text{ g CP/kg BW}^{0.60}$  per day (MP requirement of  $0.3 \text{ g CP/kg}^{0.60}$ , using the efficiency factor of 0.67).

The last route assessed by Swanson (1977) was MFP, for which it is not easy to have a clear description. For example, the definition of MFP has changed with time, from “a residue of body secretions and tissue incident to movement of food through the gastrointestinal tract” (Swanson, 1977) to the definition of Swanson (1982) adopted in the last NRC (2001) “bacteria and bacterial debris synthesized in the caecum and large intestine, keratinized cells, and a host of other compounds”. The requirement for MFP used by NRC and CNCPS is based on studies of Swanson (1977, 1982). Best correlations were obtained relative to indigestible dry matter (**DM**), but due to uncertainties related to the digestibility of DM, the most recent NRC (2001) has chosen to use DM intake (**DMI**) as the basis to determine MFP (30 g MP/kg DM intake). In addition, the NRC sub-committee estimated that rumen microbial protein (included in the calculation of MFP) should not be included as metabolic loss and, therefore, 50% of the undigested microbial protein is subtracted from this estimation (the other half is assumed to be digested in the hindgut). Therefore, in NRC (2001), the MP requirement for MFP = (DMI (kg) x 30) - 0.50 x ((bacterial MP/0.80) - bacterial MP). The CNCPS currently calculates MFP as 9% of indigestible DM (Fox et al., 2004), as previously estimated by NRC (1989), without any correction for the presence of bacteria. Therefore the CNCPS estimates of MFP are higher than those from the NRC. In addition, NRC (2001) also assumes a requirement for the endogenous flow of protein at the duodenum, but NRC also includes this flow in MP supply.

Table 1 summarizes estimated MP requirement for a “typical” 700 kg cow producing 45 kg milk/d at 3.2% CP (3.0% true protein) and eating 27 kg DM/d with the NRC (2001) and CNCPS (Fox et al., 2004) ration balancing models.

### ***Amino acids***

Two different approaches are used to determine the AA requirement. The proportional approach was put forward by NRC (2001) as the sub-committee stated that at that time, “current knowledge (on AA) is too limited to put forth a model that quantifies AA requirement for dairy cattle”. To determine the proportion of each AA needed to maximize milk protein yield or percentage, a dose-response relationship between the % of individual AA in MP supply and milk protein yield or percentage was established, using a broken stick model. The % observed at the breakpoint represents the proportion of this AA in MP supply required to maximize the targeted output. This approach adopted by NRC (2001) yielded recommendations for lysine at 7.08% and 7.24% of MP, and for methionine at 2.35% and 2.38% of MP, for maximal milk protein yield and milk protein concentration, respectively. This is also the approach adopted by the INRA ration balancing model (2007), which states similar recommendations.

On the other hand, the factorial approach cumulates the requirement for individual functions (maintenance and lactation in the current presentation) with a defined AA composition and a defined efficiency of transfer of each digested AA for each function. This is the approach used, for example, by CNCPS (Fox et al., 2004), AMTS and Amino Cow. In addition to the determination of the MP needed to fulfill each function, this approach requires the AA composition of the protein involved in each

function as well as the efficiency with which each digested AA will be used to cover that function. In CNCPS (Fox et al., 2004), milk AA composition is derived from a rather old estimation (Jenness, 1974) whereas the assumed AA composition used for endogenous urinary and MFP is based on that of whole body tissues (Ainslie et al., 1993). For scurf, whole-body tissue AA composition is used (Fox and Tedeschi, 2003), although the AA composition of keratin had been proposed (O'Connor et al., 1993).

### ***Efficiency***

In NRC (2001) and CNCPS (Fox et al., 2004), once the “raw” requirement for net protein have been determined for maintenance or lactation, they are translated into a requirement for MP supply, using a single transfer coefficient (0.67 and/or 0.65), except for MFP to which no efficiency factor is applied.

In CNCPS, to each of the maintenance and lactation processes is associated a fixed efficiency of utilization of AA, different for each AA but independent of the supply (Table 2). The efficiencies of utilization of AA for maintenance are largely derived from one article (Evans and Patterson, 1985), averaging 0.85 for all essential AA except the branched-chain AA for which it averaged 0.66. The efficiency of lactation is based on the uptake:output ratio of individual AA across the mammary gland (Fox et al., 2004). Although it is acknowledged that “AA absorbed in excess will be used less efficiently, and those absorbed at levels below requirement will be used with a higher efficiency” (Fox and Tedeschi, 2003), there is no attempt to propose variations in these efficiencies.

## **Proposed Updates to Requirements**

### ***Proteins***

As a general statement, protein requirement could be defined as the sum of all the protein needed to support proteins and AA excreted out of the body of the cow. This would include all proteins excreted out of the cow (milk, endogenous fecal protein, scurf), plus N excreted in urine but originating from digested AA (AA-derived compounds plus urea synthesized from AA catabolism). This latter amount represents the difference between 1 (100% efficiency) and the efficiency of utilization of MP or AA. This proposed approach would then eliminate the ambivalence of a so-called “maintenance” requirement which is dependent on DM intake: for example, in our typical cow, can we really refer to maintenance requirement when assessing the MFP of a cow eating 27 kg/day to maintain her high milk production?

Milk protein used to estimate protein requirement should refer to true protein, especially knowing that the proportion of non-protein N can vary with protein supply (e.g. Raggio et al., 2004). In our typical cow, the sum of endogenous urinary plus scurf represents less than 5% of the MP requirement: therefore, the current assumptions can probably be used, at least until the other major contributors to MP requirement are better sorted out. The next version of the French system in preparation, now called

Systali, has however reviewed endogenous urinary requirement and first estimations have almost doubled it. Only the NRC (2001) ration balancing model includes requirement for the flow of endogenous proteins at the duodenum. Based on the definition above, as this flow is not leaving the body of the animal, it should not be included in the requirement per se. Indeed, the fraction that will be digested and re-absorbed does not represent a cost of AA per se for the animal: only the undigested fraction flowing at the ileum and mostly recovered in the feces represents a real cost. However, adequate quantification of the contribution of endogenous protein to the duodenal flow is crucial: this contribution needs to be removed from measured duodenal flow to determine the true net supply, because the endogenous proteins, which may represent up to 15-20% of duodenal CP flow, are not a net contributor to the AA supply (Ouellet et al., 2002, 2007 and 2010).

The largest component of the so-called maintenance requirement is MFP. As discussed previously, this component currently differs substantially between NRC (2001) and CNCPS (Fox et al., 2004, Table 1). Another peculiarity of this component of requirement is that no efficiency of utilization of absorbed protein is applied to it to convert the “exported” protein into requirement. This occurs despite the clear indication given by Swanson (1977): “Furthermore, whichever portion of the fecal N is designated MFN, it is converted to maintenance requirement for protein only when modified by appropriate factors for utilization efficiency of feed proteins”. An efficiency factor was not applied as this would have yielded maintenance requirement too high for the MP supplied. This overestimation of MFP is probably due to the methods used in the studies that Swanson (1977) used to obtain that value: for example, included in these estimations of MFP is urea recycled in the rumen and captured by bacteria, which is not per se a requirement on digested proteins. Therefore, we propose to use as an estimation of MFP the ileal flow of endogenous proteins estimated by isotopic dilution in dairy cows (Lapierre et al., 2007; Ouellet et al., 2007). As a first step, these estimations were reported based on DM intake and would average 15.8 g CP/kg DM intake, and using an average proportion of true protein/CP of 0.80 and an efficiency of 0.67 (NRC, 2001), that would yield a requirement of 19 g MP/kg DM intake. Research is currently underway to update these values and determine if DM intake is the major factor affecting the magnitude of MFP.

### ***Amino acids***

When using the factorial approach, the proportions for lysine and methionine relative to MP supply proposed by NRC (2001) have been widely used. However, recent analyses conducted by the group of Dr. Schwab clearly indicate that the proportions recommended should be evaluated within each ration balancing model (Whitehouse et al., 2009, 2010a and b). These recommendations can differ substantially between models and also depending of the target, i.e. milk protein yield or milk protein concentration. For example, when assessing the milk protein concentration response, the recommendations for lysine would vary between 6.84% (AMTS) and 7.24% (NRC), depending on the ration balancing model used (Table 3). Similarly, although CNCPS is using a factorial approach, they have estimated, based on their refined feed library

(Higgs et al., 2012) and updated efficiencies of utilization, which will be used in version 6.5, a lysine and methionine requirement of 7.00 and 2.60 of MP, respectively, for maximal milk protein yield (van Amburgh et al., 2013).

When using the factorial approach, two factors need to be known to transfer the protein exported out of the body into AA requirement: the AA composition of this protein and the efficiency with which the absorbed AA will be used. Efficiency will be discussed in the following section. For milk AA composition, we propose an update using the AA composition of the reference protein of each protein family (e.g. different caseins, lactalbumin  $\alpha$ , different Ig, etc) most recently detailed in the Journal of Dairy Science (Farrell Jr et al., 2004; Lapierre et al., 2012). This update includes all the proteins secreted in the milk and not only the proteins synthesized within the mammary gland. Milk AA composition should be determined based on true protein and not CP as the non-protein N fraction of milk can vary with protein supply (e.g. Raggio et al., 2004). Therefore, adopting a constant AA composition relative to CP in milk could be misleading. Also, despite the common use of the factor 6.38 for the conversion of milk N into CP concentration, the factor 6.34 would be more appropriate (Karman and van Boekel, 1986; personal calculations). Table 4 presents the proposed update of milk AA composition.

As presented previously, MFP is another major source of proteins exported out of the cow. Proteins from endogenous origin flowing at the ileum and excreted in the feces originate from very different sources. They are either constitutive proteins (sloughed cells) or proteins exported out of the cells where they have been synthesized (saliva, enzymes, mucins; Tamminga et al., 1995): therefore, the AA composition of this protein mixture is a challenge to determine, but it is clear that the composition of empty body which is currently being used is not the most appropriate composition. In dairy cows, there are very few studies assessing either directly (Ørskov et al., 1986) or indirectly (Larsen et al., 2000) the AA composition of endogenous protein at the duodenal level and virtually no studies defining AA composition of intestinal endogenous proteins. However, some data are available in pigs for this gut segment (Jansman et al., 2002) and AA composition of intestinal secretion in pigs are close to the AA composition of duodenal flow of endogenous proteins in ruminants. Therefore, we propose, for now, an average of these values (Table 4), which should be closer to the true AA composition of endogenous secretion than that currently used. Obviously, further work is needed to improve the estimation of the AA composition of this important loss of protein.

### ***Efficiency***

Either for protein or for AA, once the exported proteins have been identified and quantified, to calculate the requirement, we need to assess with which efficiency the absorbed protein or AA will be used to support protein synthesis. Although it is widely recognized that absorbed protein is used with a lower efficiency at higher supply (Hanigan et al., 1998), it is a real challenge to integrate this variability in ration balancing models.

At the individual level, essential AA not used for anabolic functions are removed from blood circulation in specific tissues depending on the presence of the enzymes responsible for their catabolism (Lobley and Lapierre, 2003). For example, essential AA from Group 1 (histidine, methionine, phenylalanine + tyrosine) are mainly removed by the liver and very little extraction of excess AA occurs in the mammary gland or in peripheral tissues other than the amount removed to support milk protein secretion and endogenous secretions. At the opposite, for the essential AA of Group 2 (isoleucine, leucine, lysine and valine), little is removed by the liver whereas oxidation (=inefficiency) occurs in the gut, the peripheral tissues and the mammary gland (Lapierre et al., 2012). Given that removal of excess AA does not occur at the site of protein synthesis and exportation but is specifically related to tissues having the enzymes for catabolism, we have proposed that rather than using an efficiency for maintenance different from the efficiency for lactation, we could use a combined efficiency of utilization (Lapierre et al., 2007). In addition, variation of the proportion of absorbed AA removed by the different tissues and recovered in milk greatly depends on AA supply (Doepel et al., 2004; Raggio et al., 2004). Based on these observations, a meta-analysis was conducted in studies where AA supply was increased through infusions, in order to have an assessment of the increased supply independent of any ration balancing model (Doepel et al., 2004). After this first analysis, we calculated a combined efficiency of utilization for AA and MP, presented in Table 5 (Lapierre et al., 2007). The next version of CNCPS 6.5 will adopt the combined efficiencies estimated at 100% of the MP requirement (van Amburgh et al., 2013).

Therefore, the following updates are proposed:

- Milk:
  - AA composition should be based on true protein,
  - An updated AA composition is proposed.
- Metabolic Fecal Protein:
  - represents the endogenous protein losses,
  - MP requirement of 19 g MP/kg DMI, calculated based on the estimation of ileal endogenous flow is proposed,
  - AA composition based on abomasal isolates in cattle and ileal endogenous secretions in pigs is proposed.
- No need to include requirement for endogenous flows at the duodenal level as this protein synthesis can be considered similar to protein synthesis in other tissues (but this digested protein needs to be removed from net supply).
- Efficiency
  - Efficiency of utilization of MP and AA should vary with supply,
  - The mammary uptake:output ratio should not represent the efficiency of lactation,
  - A combined efficiency of AA utilization for both maintenance and lactation is proposed.

## Conclusion

The suggested recommendations are far from capturing all the complexities of the digestive and lactation processes, but they are based on the most recent knowledge of dairy cow metabolism and offer an enhanced framework to include this knowledge to improve our estimation of protein and AA requirement using current ration balancing models. Of course, they represent only approximations of complex metabolic pathways operating in dairy cows. Some aspects are not considered, especially interactions such as how changes in amount or type of energy alter outputs and efficiencies. Furthermore, as all the factors are based on empirical observations and equation fits, they do not permit different predictions for cows with different genetic potential, which may alter significantly the response to changes in the ration. Nonetheless, better appreciation of 'true' losses via digestive tract metabolism and the inclusion of a variable coefficient will yield immediate practical benefits. Adoption of such changes should not deter us from developing more mechanistic models, capable of responding to improved genetic selection, animal husbandry and feed processing technology and that can predict both within and between animal responses to changes in nutrient inputs.

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**Table 1.** Estimation of metabolizable protein (MP) requirement (requirement) for maintenance and milk in dairy cows

Function Ration balancing model <sup>1</sup>	Variables associated with MP requirement			
	Crude protein, g/d	True protein, g/d	Efficiency	MP requirement, g/d
Milk				
NRC	1440	1350	0.67	2015
CNCPS	1440	1339 <sup>2</sup>	0.65	2060
Scurf				
NRC	10	ND <sup>3</sup>	0.67	15
CNCPS	10	ND	0.67	15
Endogenous urinary				
NRC	73	ND	0.67	109
CNCPS	73	ND	0.67	109
Metabolic fecal protein				
NRC	631	ND	ND	631
CNCPS	810	ND	ND	810
Duodenal endogenous flow				
NRC <sup>4</sup>	257	128	0.67	191
CNCPS	ND	ND	ND	ND
Total requirement				
NRC				2961
CNCPS				2994

<sup>1</sup>National Research Council (NRC, 2001) and CNCPS (Cornell Net Protein and Carbohydrate System, Fox et al., 2004).

<sup>2</sup>Using a fixed proportion of non-protein N in milk of 7%.

<sup>3</sup>ND: not defined / not used.

<sup>4</sup>Assuming 1436 g of MP from bacterial origin.

**Table 2.** Coefficients of efficiency for individual amino acids (AA) for maintenance or lactation currently used by CNCPS<sup>1</sup>

Function	AA								
	Arg	His	Ile	Leu	Lys	Met	Phe	Thr	Val
Maintenance	0.85	0.85	0.66	0.66	0.85	0.85	0.85	0.85	0.66
Lactation	0.35	0.96	0.66	0.72	0.82	1.00	0.98	0.78	0.62

<sup>1</sup>Adapted from Fox et al., 2004.

**Table 3.** Optimal proportion (%) of lysine and methionine in metabolizable protein supply to maximize milk protein yield or concentration, according to different ration balancing models

Response to maximize	Ration balancing model	Amino acid	
		Lysine	Methionine
Milk protein yield	Initial NRC <sup>1</sup>	7.08	2.35
	NRC - expanded database <sup>2</sup>	6.95	2.38
	AMTS <sup>2,3</sup>	6.74	2.31
	CPM <sup>2</sup>	7.36	2.44
Milk protein concentration	Initial NRC	7.24	2.38
	NRC - expanded database	6.89	2.23
	AMTS	6.84	2.40
	CPM	7.23	2.40

<sup>1</sup>NRC (2001).

<sup>2</sup>Whitehouse et al., 2010 a and b.

<sup>3</sup>Whitehouse et al., 2009 for Met in AMTS ration balancing model.

**Table 4.** Proposed amino acid (AA) composition of milk and metabolic fecal protein (MFP)<sup>1</sup>

AA	Milk mg AA / g true protein	MFP mg AA / g CP <sup>2</sup>
Arg	37.4	32.3
His	29.0	20.0
Ile	61.3	31.5
Leu	103.6	40.1
Lys	87.6	42.4
Met	29.9	10.6
Phe	52.2	28.5
Thr	47.0	46.2
Trp	16.2	12.0
Val	69.3	43.9
Ala	35.4	41.7
Asn	42.7	67.6 <sup>3</sup>
Asp	37.8	-
Cys	9.0	19.6
Gln	96.5	96.3 <sup>3</sup>
Glu	128.8	-
Gly	20.0	122.1
Pro	103.8	68.4
Ser	67.4	51.2
Tyr	58.4	25.3

<sup>1</sup>See text for detail.

<sup>2</sup>Assuming 80% of true protein in MFP crude protein (CP).

<sup>3</sup>For MFP, Asn is the sum of Asn+Asp and Gln is the sum of Gln+Glu.

**Table 5.** Combined efficiency (maintenance plus lactation) of utilization of amino acids (AA) and metabolizable protein (MP) in relation to their optimal supply

AA	% of optimal supply			
	50%	75%	100%	125%
Arg	0.68	0.63	0.58	0.52
His	0.96	0.85	0.76	0.68
Ile	0.77	0.72	0.67	0.60
Leu	0.74	0.67	0.61	0.55
Lys	0.81	0.75	0.69	0.62
Met	0.85	0.74	0.66	0.59
Phe	0.70	0.63	0.57	0.51
Thr	0.68	0.68	0.66	0.60
Val	0.79	0.72	0.66	0.59
MP	0.72	0.67	0.62	0.56

<sup>†</sup>From the database of Doepel et al. (2004) and adapted from Lapierre et al. (2007); estimated as AA in milk protein plus the net requirement for maintenance (proportion in this paper) divided by net supply of AA.

# **SESSION NOTES**