Effects of Dietary Crude Protein on Protein and Fat Deposition in Milk-Fed Veal Calves

E. Labussiere,*†‡ S. Dubois,*† J. van Milgen,*† G. Bertrand,‡ and J. Noblet*†¹

*Institut National de la Recherche Agronomique, UMR1079 SENAH, F-35000 Rennes, France

†Agrocampus Ouest, UMR1079 SENAH, F-35000 Rennes, France

‡Institut de l'Elevage, Monvoisin, BP 85225, F-35652 Le Rheu Cedex, France

ABSTRACT

Research on veal calf production has focused on maximizing lean tissue growth. Nevertheless, limited attention has been paid to the evolution of digestive and metabolic utilization of N and energy as calves get older, whereas age at slaughter increases. The objective of this study was to determine the effects of 4 concentrations of dietary crude protein (CP) content on protein and fat deposition and energy utilization in milk-fed calves at 3 stages of fattening using the balance technique combined with heat production measurements in a respiration chamber. At each stage, 16 Prim'Holstein male calves (mean body weight at each stage: 72, 136, and 212 kg) received 4 isocaloric diets with CP contents of 76, 88, 100, and 112% of a reference CP content fixed at 20% during the first stage and 19% during the 2 later stages. After 2 wk of adaptation to their respective diets and housing conditions, the calves were placed for 1 wk in an open-circuit respiration chamber for N and energy balance measurements (first 6 d) and measurement of the fasting heat production (last day). Measurements for a stage were performed over 2 periods of 4 successive weeks. There was no effect of dietary CP on digestibility during the 2 later stages, but the low-protein diet resulted in lower digestibility coefficients for dry matter, organic matter, gross energy, CP, and crude fat during the first stage. Endogenous fecal N was estimated as 2.5 g/kg of dry matter intake irrespective of stage, and metabolic urinary N was estimated at 0.07 g/kg of body weight^{0.85} per day. Maximum N retention was 32.8, 40.5, and 44.0 g/d at stages 1, 2, and 3, respectively. The effect of protein intake on protein deposition was dependent on age of the calves, because the marginal efficiency of digestible protein utilization decreased from 64 to 18% as animals got older. Fat deposition decreased with increasing dietary CP content irrespective of stage. Total energy retention was not modified by dietary CP content. The composition

of body weight gain was affected differently for each stage, because the protein content of body weight gain increased with increasing dietary CP content during the first stage, whereas it remained constant during the other 2 stages. Fat and energy content in body weight gain decreased with increasing dietary CP irrespective of stage. These results provide a basis for estimating protein requirement of veal calves according to a factorial approach.

Key words: veal calf, protein intake, protein and fat retention, heat production

INTRODUCTION

Research on veal calf production has focused on maximizing lean tissue growth. Due to the increasing cost of milk derivatives used in milk replacers, more attention has to be devoted to maximizing the efficiency of nutrient utilization, in particular proteins, to produce lean tissue. Furthermore, optimizing dietary CP concentrations contribute to decreasing excess N excretion. Recent studies on protein requirements of veal calves have mainly focused on young animals (Blome et al., 2003; Bartlett et al., 2006). When older animals were used, growth performance was measured over longer periods of time with little focus on the evolution of digestive and metabolic utilization of nutrients and energy (Gerrits et al., 1996). Moreover, genotypes of calves have progressively changed in Europe (predominance of Prim'Holstein), and BW and age at slaughter have increased.

The changing context and the relative lack of recent data justify a reevaluation of the protein requirements of veal calves. The objective of this study was to quantify the effect of dietary CP concentration on N and energy utilization for protein and lipid deposition and on heat production (HP) in veal calves over the whole rearing period (25 wk).

MATERIALS AND METHODS

The present experiment complied with French ethic laws and was conducted under the direction of J. No-

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¹Corresponding author: jean.noblet@rennes.inra.fr

blet (authorization number 04739) and G. Bertrand (authorization number 07558).

Experimental Design

This experiment was designed to determine the effect of 4 concentrations of dietary protein on protein and lipid deposition and on HP in veal calves during 3 stages: stage 1 (from 5 to 8 wk in rearing), stage 2 (from 13 to 16 wk), and stage 3 (from 21 to 24 wk), that is, a 4-wk delay between successive stages. Week 1 corresponds to the first week after purchasing and arrival at the facilities at 7 to 15 d of actual age. The measurements were conducted on 4 calves per protein concentration at each stage and consisted of a 6-d N and energy balance followed by a fasting day for estimating the fasting HP (**FHP**). Because only 2 large respiration chambers were available, 2 balances could be performed weekly. Two successive batches of calves were used, and measurements were alternated between batches; calves of the second batch were purchased 4 wk after the first batch. The average age for balance measurements was equivalent for the 4 dietary treatments and 2 batches.

Experimental Diets

Four grower diets differing in their CP contents were used during stage 1, and 4 finisher diets differing in their CP contents were used during stages 2 and 3. Diets were formulated to include skim milk powder, 50% fat-enriched skim milk powder (fat constituted 80% tallow and 20% coconut oil), and lactose (Table 1). The CP concentrations were considered relative to a reference CP concentration, which was 20% for grower diets and 19% for finisher diets. For each type of diet, the 4 CP concentrations contained 76, 88, 100, and 112% of the reference concentration of CP and were referred to as G76, G88, G100, and G112 for the grower diets and F76, F88, F100, and F112 for the finisher diets. Differences in CP concentrations were achieved by substituting skim milk powder for the 50%-fat enriched skim milk powder plus lactose so that CP replaced a mixture of lactose and fat at the same gross energy concentration. Titanium dioxide was included in the finisher diets as an indigestible marker to correct for possible incomplete feces collection. Because feces were collected without losses, marker data were not further used in the calculations. Diets were supplemented with L-lysine, DL-methionine, L-threonine, and L-tryptophan to achieve an ideal AA profile as proposed by Labussière et al. (2007).

Liquid milk was reconstituted just before distribution by dissolving the diets in hot water at a concentration increasing from 130 to 175 g of DM/kg of reconstituted

milk as the calf got older. This milk was offered at a temperature ranging from 45 to 50°C in 2 equal meals at 0845 and 1800 h. Quantities of DM offered daily and calf BW during measurements are given in Table 2. During the fasting day, calves only received a morning meal with diets they had received during the previous 6 d and were fasted thereafter. To limit disturbance in performance due to the insufficient protein supply, calves were offered the reference diet (G100 or F100) when they were not in the adaptation or measurement period.

Animals, Housing, and Management

Two batches of 14 male Prim'Holstein calves were used in this experiment. Measurements were conducted on 8 calves per batch and per stage. Three calves of each batch were assigned to a CP concentration allowing 2 supplementary calves per batch. These calves could be used to replace others of the same batch in case of problems. Each week, 2 calves receiving 2 different CP concentrations were moved from the pen to cages with a wood-slatted floor at the experimental station of the Institut de l'Élevage (Le Rheu, France). After 1 wk, calves were transferred to the Institut National de la Recherche Agronomique (**INRA**) facilities (Saint-Gilles, France; 10 km distance from Le Rheu) for further adaptation and measurements. Upon arrival, they were housed for a 1-wk adaptation period using the same metabolism cages. The cages were placed in the same room but separated by a curtain to avoid visual contacts between the 2 animals. Calves were bucket-fed automatically without human intervention just before distribution. The automated feeding procedure consisted of distributing the reconstituted milk through the bottom of the bucket. This milk was previously stored and constantly stirred in a plastic can. After 10 min, refusals were pumped out through the bottom of the bucket and 1 L of hot water (at approximately 60°C) was poured in the bucket and pumped to the plastic can to rinse the system. Refusals and rinse water were collected together and stored. Two days before entrance in the respiration chamber, a harness with plastic bag was attached to the calves to allow total collection of feces.

During the measurement week, the calf in its metabolism cage was placed in a 12-m³ open-circuit respiration chamber (Vermorel et al., 1973). The cage was mounted on force sensors, which produced an electrical signal indicative for the physical activity of the calf. The position of the animal (standing or lying) was evaluated using an infrared beam placed across the cage at the bottom of the hip. The temperature and relative humidity in the chamber were maintained constant at

Table 1. Composition of milk replacers

Item ¹	Stage 1				Stages 2 and 3			
	G76	G88	G100	G112	F76	F88	F100	F112
Ingredient, g/kg								
Skim milk powder (SMP)	214.5	287.0	359.1	426.6	181.5	249.3	319.0	385.0
50%fat SMP	369.9	352.1	333.9	315.3	375.1	356.4	338.4	323.7
Lactose	339.5	290.9	242.9	201.0	364.0	322.0	277.3	230.0
Wheat starch	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0
Lysine	—	—	—	—	0.2	0.2	—	—
Methionine	2.0	2.3	2.6	2.9	2.0	2.3	2.5	2.8
Threonine	0.8	0.9	1.1	1.2	1.3	1.4	1.4	1.7
Tryptophan	0.2	0.2	0.3	0.3	0.3	0.3	0.3	0.3
Minerals and vitamins ²	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0
Iron mixture ³	1.0	1.0	1.0	1.0	0.3	0.3	0.3	0.3
Calcium formiate	11.0	8.0	5.0	2.0	11.0	8.0	5.0	3.0
Monopotassium phosphate	11.0	8.0	5.0	2.0	11.0	8.0	5.0	3.0
Salt	7.0	7.0	6.0	5.0	8.0	7.0	6.0	5.0
Emulsifier ⁴	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2
Silica	1.8	1.4	1.8	1.4	2.0	1.6	1.6	2.0
Titanium dioxide	—	—	—	—	2.0	2.0	2.0	2.0
DM, g/kg	954	954	953	959	962	960	962	960
Chemical composition, ⁵ g/kg of DM								
Ash	64	65	67	64	64	63	63	64
CP	162	189	213	237	151	174	196	221
Crude fat	197	185	174	164	195	184	172	163
Lactose	592	573	557	541	592	584	562	546
Gross energy, MJ/kg of DM	20.99	20.95	20.99	20.93	20.74	20.71	20.79	20.79

¹The CP content of diets G76 to G112 and F76 to F112 was determined as 76 to 112% of a reference CP content of 200 and 190 g/kg for grower and finisher diets, respectively.

²The minerals and vitamins mixture provided (per gram of mixture): magnesium, 45 mg; retinol, 2,000 IU; cholecalciferol, 400 IU; α tocopherol, 8 mg; ascorbic acid, 15 mg; thiamin, 1 mg; riboflavin, 1 mg; pyridoxin, 0.8 mg; cyanocobalamin, 0.008 mg; niacin, 4 mg; pantothenic acid, 2 mg; menadione, 0.25 mg; biotin, 0.01 mg; folic acid, 0.15 mg; choline, 50 mg; betaine, 20 mg; iron, 1 mg; copper, 1 mg; zinc, 4 mg; manganese, 5 mg; cobalt, 0.04 mg; iodine, 0.045 mg; selenium, 0.02 mg, Lactalis Industrie, Bourgbarré, France.

³The iron mixture provided (per gram of mixture): thiamin, 4 mg; cyanocobalamin, 0.08 mg; folic acid, 1 mg; iron, 18.5 mg; copper, 4.8 mg; cobalt, 0.5 mg, Lactalis Industrie.

⁴The emulsifying agent contained soy fatty acids, polyethylene glycol, glycerol (60%), and silica (40%), Cognis, Düsseldorf, Germany.

⁵As measured.

18°C and 70%, respectively. A 12-h lighting time span (from 0730 to 1930 h) was used. The 2 separate respiration chambers were equipped with microphones and speakers so that calves could hear each other. Calves were offered the reconstituted milk as in the adaptation week.

Measurements

Calves were weighed upon arrival at the INRA facilities and at entrance in the respiration chamber before

the morning meal. During the first stage of measurements, all calves were weighed on the morning before and after the fasting day. This procedure required the complete opening of the respiration chamber and may also cause stress to the animal. Because of this, this procedure was partly abandoned for the 2 later stages in which calves of the first batch were still weighed before and after fasting, whereas calves of the second batch were only weighed after the fasting day: BW of these calves on the morning before fasting was estimated using a linear relationship between BW prior

Table 2. Age (week of fattening), milk replacer offered, and mean BW of veal calves during balance measurements

Item	Stage 1				Stage 2				Stage 3			
	5 wk	6 wk	7 wk	8 wk	13 wk	14 wk	15 wk	16 wk	21 wk	22 wk	23 wk	24 wk
Milk replacer offered, g of DM/d	1,132	1,279	1,400	1,508	1,996	2,107	2,217	2,276	2,783	2,792	2,848	2,871
Average BW, kg	62	67	76	83	122	131	141	149	200	207	221	221

and after fasting obtained from the calves of the first batch ($BW_{\text{prior fasting}} = 0.43 + 1.01 \times BW_{\text{after fasting}}$, $R^2 = 0.99$).

The quantity of milk offered to each calf when housed at the INRA facilities was weighed, and milk replacer was sampled over the balance period. Samples were pooled by diet and stage. Diluted refusals were weighed for each calf after each meal, and a 20-mL sample was frozen. Feces were collected and weighed daily, stored at -20°C , and pooled per calf over the 6-d period. Urine was collected in buckets containing 120 mL (stage 1) or 240 mL (stages 2 and 3) of H_2SO_4 (1.8 mol/L) to prevent volatilization of NH_3 and weighed daily. An aliquot was taken and pooled per calf over the 6-d balance period and stored at $+4^\circ\text{C}$ awaiting further analysis.

Gas concentrations (CO_2 , O_2 , and CH_4) of outgoing air and ventilation rate were recorded continuously according to methods described by van Milgen et al. (1997). The O_2 concentration was measured with a paramagnetic differential analyzer (Oxymat 6, Siemens AG, Munich, Germany), whereas the CO_2 concentration was measured with an infrared analyzer (Ultramat 6, Siemens AG, or Unor 600, Maihak AG, Hamburg, Germany). A single CH_4 analyzer (Unor 6N, Maihak AG) was available for the 2 respiration chambers, and CH_4 concentration was measured during the first 3 d for one respiration chamber and during the following 3 d for the other one. Gas extraction rate was measured with a mass gas meter (Teledyne Brown Engineering, Hampton, VA). Gas concentrations, the signals of the force sensors, the weight of the distribution recipient, gas flow rate, temperature, and relative humidity in the respiration chamber were measured 60 times per second, averaged over 10-s intervals, and recorded for further calculations. Ammonia losses in the air recovered in condensed water and outgoing air were collected according to methods described by Noblet et al. (1987).

Chemical Analyses

Samples of feed (1 per diet) were analyzed for DM, ash, N, ether extract, lactose, and gross energy contents according to standard methods (AOAC, 1990); N content was also analyzed on feed samples taken weekly, and CP content was calculated assuming a converting factor equivalent to 6.38. Samples of diluted refusals were analyzed for DM, and its DM composition was supposed to be identical to the feed offered. Fecal samples were similarly analyzed for DM, ash, ether extract, N, and gross energy content. Samples of urine were analyzed for N content on fresh material. Gross energy content in the urine was obtained after freeze-drying approximately 30 mL in polyethylene bags. The NH_3

content of condensed water and extracting air was determined on fresh material using an enzymatic method (Enzytec fluid, Scil Diagnostics GmbH, Martinsried, Germany).

Calculations

Mean growth rate of the calf for the overall adaptation and balance period (12 d) was calculated using estimated BW on the morning after the arrival at the INRA facilities and the BW on the morning of the fasting day. The former was obtained by applying an adjustment function to the BW measured at the arrival at the facilities (calves arrived in the middle of the day). The adjustment function ($0.24 + 0.98 \times BW_{\text{at arrival}}$; $R^2 = 0.99$) was determined from data obtained from another trial in which calves were actually weighed twice (at arrival and at the next day before feeding). Growth rate was also calculated for the balance period only (i.e., during the presence in the respiration chamber and while fed). Assuming a constant growth rate, this latter value was used to estimate each morning BW over the balance measurement period.

The DMI and apparent digestibility coefficients of DM, OM, N, gross energy, and ether extract were calculated according to standard procedures. Nitrogen retention (RN) of each calf was calculated as the difference between ingested N and N losses in feces, urine, condensed water, and $\text{NH}_3\text{-N}$ in extracted air (called evaporated). Digestible energy (DE) intake was calculated as the difference between gross energy intake and energy excreted in the feces, whereas ME intake was calculated as the difference between DE and energy losses in the urine. Methane production was negligible and therefore not included in calculations. Total HP was calculated from O_2 consumption and CO_2 production according to the formula of Brouwer (1965). The first day in respiration chamber was considered as an adaptation day, and all calculations were carried out for the 5 subsequent days. Energy retention was calculated as the difference between daily ME intake and average HP. Assuming an energy content of the protein gain of 23.6 kJ/g (van den Borne et al., 2006b), energy retained as protein was calculated from the N balance (energy retained as protein = $\text{RN} \times 6.25 \times 23.6$), and energy retained as fat was calculated as the difference between total energy retained and energy retained as protein. Fat deposition was calculated assuming an energy content of 39.7 kJ/g. The protein and lipid concentrations of the BW gain were calculated by relating deposition to mean growth rate over the 12 consecutive days of adaptation and measurements.

Simultaneous measurements of O_2 and CO_2 concentrations in the respiration chamber, signals of force

sensors, feed intake (time of distribution and ingested quantity), and physical characteristics of gas exchanges in the chamber were used to calculate the components of HP according to the modeling approach of van Milgen et al. (1997). In brief, the variations in O₂ and CO₂ concentrations in the respiration chamber were related to events occurring in the chamber and resulting in gas exchanges due to feed intake and physical activity in addition to the gas exchanges corresponding to basal metabolic rate. The HP due to physical activity, feed intake (short-term effect of feeding), and resting metabolism were calculated from the respective volumes of O₂ consumption and CO₂ production using the formula of Brouwer (1965) excluding urinary N losses. During the fasting day, the O₂ consumption and CO₂ production during the last 12 h were used to estimate the FHP using the method described by van Milgen et al. (1997), corresponding to the asymptotic value of metabolic rate at zero activity. The difference between HP due to resting metabolism and FHP was assumed to correspond to a long-term effect of feeding and, combined with the short-term effect of feeding, allows calculating the total thermic effect of feeding. Results about FHP and HP due to physical activity have been combined with data of another trial and published by Labussière et al. (2008); they will not be considered in detail here. All energy measurements are expressed relative to BW^{0.85} per day (Labussière et al., 2008).

Statistical Analysis

Data were analyzed separately for stage 1 but together for stages 2 and 3, according to the type of diets (grower or finisher) the calves received. Data for stage 1 were analyzed including the effects of diet and week of measurement, and those for stages 2 and 3 were analyzed including the effects of diet, stage, week of measurements (within stage), and interaction between diet and stage. The PROC GLM of SAS (2004) was used according to the following models:

$$Y = \mu + D + W + \varepsilon \text{ for stage 1,}$$

$$Y = \mu + D + S + W(S) + D \times S + \varepsilon \text{ for stages 2 and 3,}$$

where Y = the dependent variable; μ = the intercept; D = the effect of diet; W = the effect of week of measurements within a stage; S = the effect of stage of fattening (only for stages 2 and 3); and ε = an error term. Equality of LSM was tested according to a Student test.

Endogenous N losses were considered to be proportional to DM intake (Davis and Drackley, 1998; NRC,

2001) and estimated from the relationship between digestible N (DN) and N intake, expressed per kilogram of DMI. The effects of stage of fattening on both the intercept and the slope were tested. The maintenance N requirement (recovered as metabolic urinary N) was estimated from the relationship between RN and DN for the calves (n = 11 for stages 1 and 2 and n = 4 for stage 3) receiving quantities of DN below the requirement for maximal growth according to NRC (2001). Because metabolic urinary N was assumed to depend on metabolic body size, DN and RN were expressed per kilogram of BW^{0.85} (Labussière et al., 2008). The effect of stage of fattening was not considered due to the decreasing number of values as stage increased. Nitrogen balances were also pooled across stages, and a linear relationship between RN and DN was used in the following model:

$$RN = S \times DN + S + \varepsilon,$$

where S = the effect of stage and ε = an error term. Equality of parameters across stages was tested using PROC GLM of SAS (2004).

RESULTS

Composition of the diets is given in Table 1, and characteristics were as anticipated. There were no major difficulties during the balance measurements. Four calves had some feed refusals or difficulties of adaptation during the adaptation week at INRA; they were replaced by other calves that received the same dietary treatment.

Growing Stage

The results given in Table 3 indicate that mean BW, DMI, and BW gain over the growing period were not affected by dietary CP concentration and averaged 71.9 kg, 1,300 g of DM/d, and 0.98 kg/d, respectively. Both BW and DMI increased with time. Apparent fecal digestibility coefficients for DM, OM, gross energy, CP, and crude fat were lower ($P < 0.05$) for diet G76 than for diet G100. Consequently, the DE content of diet G76 was lower than the other grower diets ($P = 0.03$). The metabolizability of DE was not affected by CP concentration and averaged 97.1%, but it decreased from 97.4 (average value for wk 5 to 7 of fattening) to 96.4% during wk 8 of fattening ($P = 0.04$). Consequently, the ME content of diet G76 was the lowest ($P = 0.01$).

According to the experimental strategy, N intake increased with dietary CP content from 32.4 to 48.8 g/d (Table 4). Daily fecal N excretion was not affected

Table 3. Effect of dietary CP concentration on performance and apparent fecal digestibility during stage 1 in veal calves (n = 16)

Item	Diet ¹				SEM	P-value	
	G76	G88	G100	G112		Diet	Week
BW, kg	69.6	71.2	72.7	74.2	2.2	0.20	<0.01
DM intake, g/d	1,289	1,302	1,295	1,312	39	0.81	<0.01
BW gain, ² kg/d	0.90	0.97	0.95	1.09	0.03	0.20	0.54
Digestibility coefficients, %							
DM	94.9 ^b	96.1 ^{ab}	97.2 ^a	95.7 ^b	0.3	0.02	0.92
OM	95.6 ^b	96.7 ^{ab}	97.7 ^a	96.4 ^{ab}	0.3	0.04	0.93
Gross energy	94.3 ^b	95.8 ^a	96.9 ^a	95.7 ^a	0.3	0.03	0.84
CP	89.5 ^b	93.3 ^a	95.1 ^a	93.0 ^a	0.7	0.02	0.75
Crude fat	92.8 ^b	94.3 ^{ab}	96.1 ^a	95.8 ^a	0.5	0.04	0.46
ME:DE, %	96.7	97.4	96.9	97.6	0.2	0.13	0.04
Energy values, MJ/kg of DM							
DE	19.67 ^b	20.05 ^a	20.26 ^a	20.03 ^a	0.07	0.03	0.75
ME	19.02 ^b	19.53 ^a	19.64 ^a	19.55 ^a	0.08	0.01	0.51

^{a,b}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Crude protein concentrations in diets: G76 = 162 g/kg of DM; G88 = 189 g/kg of DM; G100 = 213 g/kg of DM; G112 = 237 g/kg of DM.

²Body weight gain calculated over the combined adaptation and balance periods.

by CP concentration or week of measurement and averaged 2.9 g/d. Urinary N excretion increased from 6.7 to 12.4 g/d as dietary CP content increased ($P < 0.01$). Urinary N also increased with age from 7.8 to 11.9 g/d ($P < 0.01$). The quantities of N recovered in the air extracted from the respiration chamber and in the condensed water were constant and negligible (0.1 g/d). Nitrogen retained in the body increased from 22.3 to 32.8 g/d with CP concentration in the diet ($P < 0.01$). Expressed as a percentage of DN, RN was not affected by CP concentration and averaged 74.5%.

As indicated in Table 5, daily ME intake and HP (kJ/kg of BW^{0.85} per day) were not affected by CP concentration and tended to increase with time ($P = 0.08$ and $P = 0.06$, respectively). Components of HP were neither affected by concentration of CP nor by week of measurement. Retained energy was not significantly affected by dietary CP concentration, but energy retained as protein increased from 89 to 125 kJ/kg of BW^{0.85} per day ($P < 0.01$), whereas energy retained as lipid was decreased from 157 to 102 kJ/kg of BW^{0.85} per

day ($P < 0.01$) when CP concentration was increased from the lowest to the highest concentration. The respiratory quotient was not affected by CP concentration, although the value for diet G76 was numerically greater (0.96 vs. 0.94; $P = 0.18$).

Protein deposition increased from 139 to 205 g/d (Table 5, $P < 0.01$), whereas lipid deposition decreased from 146 to 99 g/d ($P < 0.01$) with increasing CP concentration in the diet. Consequently, the protein content of BW gain increased from 154 to 187 g/kg ($P = 0.01$), whereas the lipid content decreased from 163 to 90 g/kg ($P < 0.01$). The energy content of gain tended to decrease as dietary CP content increased ($P = 0.08$). Protein and fat deposition increased from 149 to 197 g/d ($P < 0.01$) and from 107 to 137 g/d ($P = 0.04$), respectively, between wk 5 and 8.

Finishing Stages

During stages 2 and 3, mean BW of the calves during measurement periods was not affected by diets (Table

Table 4. Effect of dietary CP on N utilization during stage 1 in veal calves (n = 16)

Item	Diet ¹				SEM	P-value	
	G76	G88	G100	G112		Diet	Week
N balance, g/d							
N intake	32.4 ^d	38.5 ^c	43.2 ^b	48.8 ^a	2.0	<0.01	<0.01
N excretion							
Feces	3.3	2.5	2.2	3.4	0.2	0.09	0.52
Urine	6.7 ^b	8.5 ^b	11.0 ^a	12.4 ^a	0.7	<0.01	<0.01
Evaporated	0.1	0.1	0.1	0.1	0.1	0.86	0.83
Total	10.1 ^c	11.1 ^{bc}	13.3 ^b	15.9 ^a	0.8	<0.01	<0.01
N retained	22.3 ^c	27.3 ^b	29.9 ^{ab}	32.8 ^a	1.3	<0.01	<0.01
N retained, % of digested N	76.2	76.3	73.1	72.5	1.0	0.46	0.59

^{a-d}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Crude protein concentrations in diets: G76 = 162 g/kg of DM; G88 = 189 g/kg of DM; G100 = 213 g/kg of DM; G112 = 237 g/kg of DM.

Table 5. Effect of dietary CP on energy balance, respiratory quotient, and nutrient deposition in veal calves during stage 1 (n = 16)

Item	Diet ¹				SEM	P-value	
	G76	G88	G100	G112		Diet	Week
Energy balance, kJ/kg of BW ^{0.85} per day							
ME intake	671	684	668	666	6	0.69	0.08
Heat production ²							
As FHP	316	318	321	330	4	0.51	0.15
As AHP	55	59	55	57	2	0.96	0.53
As TEF	55	52	54	52	3	0.96	0.16
Total	426	429	431	439	5	0.66	0.06
Retained energy							
As protein	89 ^c	108 ^b	115 ^{ab}	125 ^a	4	<0.01	0.50
As fat	157 ^a	147 ^a	122 ^b	102 ^c	6	<0.01	0.57
Total	246	255	237	227	5	0.24	0.54
Adjusted ³	244	248	239	232	5	0.24	0.40
Respiratory quotient	0.96	0.95	0.94	0.94	0.003	0.18	0.76
Nutrient deposition, g/d							
Protein	139 ^c	171 ^b	187 ^{ab}	205 ^a	8	<0.01	<0.01
Lipid	146 ^a	139 ^{ab}	117 ^{bc}	99 ^c	6	<0.01	0.04
BW gain composition, /kg of gain							
Protein, g	154 ^b	178 ^a	198 ^a	187 ^a	6	0.01	0.06
Lipid, g	163 ^a	145 ^{ab}	124 ^b	90 ^c	8	<0.01	0.52
Energy, MJ	10.1	10.0	9.6	8.0	0.3	0.08	0.30

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Crude protein concentrations in diets: G76 = 162 g/kg of DM; G88 = 189 g/kg of DM; G100 = 213 g/kg of DM; G112 = 237 g/kg of DM.

²FHP = fasting heat production; AHP = activity heat production; TEF = thermic effect of feeding.

³Retained energy was adjusted for the same ME intake and AHP (respectively, 672 and 57 kJ/kg of BW^{0.85} per day, i.e., average values for stage 1).

6) and averaged 136 and 212 kg ($P < 0.01$) during stages 2 and 3, respectively. Dietary CP concentration did not affect DM intake, which increased from 2,106 to 2,757 g of DM/d between stages 2 and 3. The BW gain increased from 1.17 to 1.45 kg/d when dietary CP content increased during stage 2, but it remained constant and averaged 1.44 kg/d during stage 3 ($P = 0.05$). There was no effect of stage, diet, or week on the apparent fecal digestibility coefficients of OM and gross energy, which were all greater than 93%. The digestibility of CP of the finisher diets was numerically lower than during stage 1 but did not differ between diets or stages and averaged 91.3%. The digestibility coefficient of fat was not affected by dietary CP content ($P = 0.07$), except that diets F88 and F112 gave extreme results during stage 2. The metabolizability of DE was lower during stage 3 than during stage 2 ($P = 0.04$) but did not differ between diets. The DE content of the diet was lower with diet F88 than with diet F112 ($P = 0.04$). The ME content of the finisher diets was greater in stage 2 than in stage 3 ($P = 0.03$).

As expected, daily N intake was affected by stage, diet, and week (Table 7, $P < 0.01$). Fecal N excretion was greater during stage 3 than during stage 2 (7.2 vs. 5.0 g/d; $P < 0.01$), but it did not differ between diets or week of measurement within a stage. Total N excretion increased during stages 2 and 3 when the CP concentration in the diet increased ($P < 0.01$). This

was mainly due to the increased N excretion in the urine ($P < 0.01$). Despite significant treatment effects, evaporated N remained a small fraction of N excretion in stage 2 and 3. Nitrogen retention was greater during stage 3 than during stage 2 (42 vs. 37 g/d), but it only tended to increase with the dietary CP concentration ($P = 0.06$). When expressed as a percentage of DN, RN decreased from 72.5 with F76 during stage 2 to 49.5% with diet F112 during stage 3 as CP concentration in the diet increased and as animals got older ($P < 0.01$).

According to the experimental design, ME intake (kJ/kg of BW^{0.85} per day) was equivalent for all diets within a stage and was greater during stage 2 than during stage 3 (Table 8, 611 vs. 529 kJ/kg of BW^{0.85} per day, $P < 0.01$). The total HP was not affected by dietary CP concentration but differed between stages with greater values during stage 2 than during stage 3 (400 vs. 363 kJ/kg of BW^{0.85} per day, $P < 0.01$). This was mainly due to a greater FHP (305 vs. 272 kJ/kg of BW^{0.85} per day, $P < 0.01$). Total energy retention was lower during stage 3 than during stage 2 (211 vs. 166 kJ/kg of BW^{0.85} per day, $P < 0.01$). Energy retained as protein did not differ between diets but was lower during stage 3 than during stage 2 (65 vs. 84 kJ/kg of BW^{0.85} per day, $P < 0.01$). During both stages, energy retained as fat was greater for diet F76 compared with the other diets ($P < 0.01$), and values were greater dur-

Table 6. Effect of dietary CP on performance and apparent fecal digestibility during stages 2 and 3 in veal calves (n = 32)

Item	Stage 2				Stage 3				SEM	P-value			
	F76 ¹	F88 ¹	F100 ¹	F112 ¹	F76	F88	F100	F112		Stage	Diet	Week	Diet × stage
BW, kg	130.9	135.9	138.2	138.9	208.2	211.9	216.0	213.0	7.1	<0.01	0.19	<0.01	0.95
DM intake, g/d	2,113	2,101	2,128	2,081	2,795	2,781	2,751	2,702	61	<0.01	0.31	<0.01	0.70
BW gain, ² kg/d	1.17 ^b	1.25 ^b	1.53 ^a	1.45 ^a	1.45 ^a	1.33 ^{ab}	1.53 ^a	1.44 ^a	0.03	0.03	<0.01	0.61	0.05
Digestibility coefficients, %													
DM	95.0	94.3	96.0	96.3	94.5	95.0	95.0	95.5	0.2	0.30	0.06	0.70	0.33
OM	96.0	95.3	96.8	97.3	95.6	96.0	95.3	96.5	0.2	0.27	0.22	0.93	0.37
Gross energy	94.5	93.5	95.8	96.3	94.5	95.0	93.8	95.5	0.3	0.57	0.18	0.96	0.17
CP	91.0	89.3	92.5	93.8	90.3	91.3	90.3	92.3	0.4	0.50	0.18	0.97	0.39
Crude fat	93.3	90.8	94.3	96.3	92.8	94.0	92.5	94.5	0.4	0.81	0.07	0.99	0.11
ME:DE, %	93.8	93.5	95.0	95.5	92.5	91.8	94.0	93.0	0.4	0.04	0.25	0.34	0.89
Energy values, MJ/kg of DM													
DE	20.00 ^a	19.50 ^{ab}	20.00 ^a	20.00 ^a	19.50 ^{ab}	19.25 ^b	19.75 ^{ab}	20.00 ^a	0.08	0.10	0.04	0.80	0.69
ME	18.50	18.00	19.25	19.25	18.00	18.00	18.25	18.50	0.13	0.03	0.06	0.57	0.50

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Crude protein concentrations in diets: F76 = 151 g/kg of DM; F88 = 174 g/kg of DM; F100 = 196 g/kg of DM; F112 = 221 g/kg of DM.

²Body weight gain calculated over the combined adaptation and balance periods.

Table 7. Effect of dietary CP on N utilization during stages 2 and 3 in veal calves (n = 32)

Item	Stage 2				Stage 3				SEM	P-value			
	F76 ¹	F88 ¹	F100 ¹	F112 ¹	F76	F88	F100	F112		Stage	Diet	Week	Diet × stage
N balance, g/d													
N intake	49.5 ^g	56.8 ^f	65.3 ^e	71.8 ^d	66.5 ^e	76.7 ^c	85.5 ^b	93.6 ^a	2.5	<0.01	<0.01	<0.01	0.32
N excretion													
Feces	4.4	6.0	4.7	4.6	6.4	6.9	8.1	7.4	0.3	<0.01	0.63	0.94	0.51
Urine	12.2 ^f	16.2 ^{ef}	20.9 ^{de}	26.5 ^{cd}	20.1 ^e	28.1 ^{bc}	32.8 ^b	42.2 ^a	1.7	<0.01	<0.01	0.30	0.32
Evaporated	0.1 ^e	0.2 ^{de}	0.2 ^e	0.2 ^{de}	0.4 ^{cd}	0.7 ^b	0.6 ^{bc}	1.0 ^a	0.1	<0.01	<0.01	0.50	0.03
Total	16.7 ^f	22.4 ^e	25.8 ^{de}	31.3 ^{cd}	26.9 ^{de}	35.7 ^c	41.5 ^b	50.7 ^a	1.9	<0.01	<0.01	0.16	0.13
N retained	32.8	34.4	39.5	40.5	39.6	41.0	44.0	42.9	0.9	<0.01	0.06	0.97	0.76
N retained, % of digested N	72.5 ^a	67.8 ^{ab}	65.3 ^{abc}	60.3 ^{bc}	66.0 ^{abc}	58.8 ^{bcd}	57.3 ^{cd}	49.5 ^d	1.5	<0.01	<0.01	0.80	0.92

^{a-f}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Crude protein concentrations in diets: F76 = 151 g/kg of DM; F88 = 174 g/kg of DM; F100 = 196 g/kg of DM; F112 = 221 g/kg of DM.

ing stage 2. The respiratory quotient was not affected by stage or diet and averaged 0.93.

The protein content of BW gain did not vary with diet or stage and averaged 178 g/kg (Table 8). The lipid and energy contents of BW gain decreased with increasing CP content of the diet ($P < 0.01$).

Utilization of N from Grower and Finisher Diets

The relationship between daily DN and N intake (g/kg of DM intake per day) is presented in Table 9. There was no effect of stage of fattening on the intercept or slope of the regression. The intercept differed significantly from 0 (-2.5 g/kg of DM intake, $P < 0.01$), whereas the slope was not different from unity. As explained earlier, the regression between RN and DN (g/kg of BW^{0.85} per day) included only the data of calves that received DN amounts lower than their theoretical N requirements. The intercept of the relation was not different from 0, whereas the slope was 0.81 ($P < 0.01$). Moreover, the N content of BW gain estimated by regression was 28.3 g/kg (i.e., 177 g of protein/kg, $P < 0.01$) and did not depend on stage of growth.

The linear relationships between RN and DN (g/d) are illustrated in Figure 1. The slope of the regression decreased from 0.64 ($P < 0.01$) at stage 1 to 0.40 ($P < 0.01$) and 0.18 ($P = 0.02$) at stages 2 and 3, respectively. The slopes differed between stages 1 and 2 ($P = 0.04$) and tended to differ between stages 2 and 3 ($P = 0.10$).

DISCUSSION

Digestive Utilization of Diets

For both grower and finisher diets, the digestibility coefficients for DM and energy were greater than 93%. This is due to the high digestibility of skim milk and is consistent with earlier reports (Roy et al., 1970; Ternouth et al., 1985; Guilloteau et al., 1986). Nevertheless, digestibility coefficients for nutrients of the low-protein diet were always the lowest during stage 1, which may be due to the greater concentration of carbohydrates, causing digestive disturbances (Lodge and Lister, 1973). In addition, the digestibility of CP is an apparent value, and values are logically lower for the low-CP diets during stage 1 due to a greater proportion of endogenous secretions in excreted N. The daily amount of fecal N at each stage remained constant for all diets, which means that the true fecal digestibility of dietary CP was 100% as also estimated in Table 9 (Tolman and Beelen, 1995). Therefore, the N recovered in feces was only of endogenous origin; the 2.5 g of endogenous N/kg of DMI (Table 9) is slightly greater than values

reported before for veal calves (2.2 g/kg of DMI; Davis and Drackley, 1998; 1.9 g/kg of DMI; NRC, 2001; 2.0 g/kg of DMI; van den Borne et al., 2006b).

Utilization of Digestible Dietary Protein

Traditionally, part of the urinary N is considered as a component of the maintenance N requirements. This latter part was estimated in our experiment as 0.07 g/kg of BW^{0.85} per day, which does not differ from 0 and is in the lower range of the literature values (Labussière et al., 2007). Nevertheless, the range of variation in DN might not have been sufficient to precisely estimate this component, which also appears variable in the literature (0.10 to 0.20 g/kg of BW^{0.75} per day). Additionally, our value was expressed as a function of BW^{0.85}, whereas literature data were expressed as BW^{0.75}. Because of difference in scaling, our estimate (expressed as g/d) remains close to the lower bound of literature data and increases from 2.0 to 7.6 g/d when BW increases from 50 to 250 kg, whereas the higher bound of the literature data increases up to 12.6 g/d for a 250-kg BW calf.

A decrease in the efficiency of utilization of DN with age or BW has been observed previously (van Weerden, 1972; Labussière et al., 2007). Nevertheless, the maximum values observed in the present study (76, 73, and 66% for stages 1, 2, and 3, respectively) are in the upper range of values reported in the literature, which range from 60 to 70% for grower calves (Ternouth et al., 1985; Diaz et al., 2001; Blome et al., 2003; Bartlett et al., 2006) to 55 to 60% for finisher calves (Gerrits et al., 1996; van den Borne et al., 2006b). We used milk proteins supplemented with AA to obtain an optimal AA profile (Labussière et al., 2007). This may have improved the efficiency of protein utilization. Moreover, maximum N utilization was obtained with the lowest DN intake in agreement with Donnelly and Hutton (1976a). Efficiency values of DN utilization reported in the literature have been usually obtained at greater concentrations of DN (48 to 63 g/d, Ternouth et al., 1985; 73 to 89 g/d, Diaz et al., 2001; 80 g/d, van den Borne et al., 2006b) or lower concentrations of ME intakes (500 kJ/kg of BW^{0.85} per day, Blome et al., 2003; 600 to 625 kJ/kg of BW^{0.85} per day, Bartlett et al., 2006) when considering calves of similar BW than those in our study. These conditions may contribute to decrease the efficiency of utilization of DN. When considering calves receiving DN amounts below their theoretical requirements (NRC, 2001), efficiency of utilization of DN for growth above maintenance equaled 81% (Table 9). This value is close to the biological value of milk protein (80%; NRC, 2001) and therefore represents the maximum gross efficiency of utilization of DN above maintenance. This latter value was close to 80% dur-

Table 8. Effect of dietary CP on energy balance, respiratory quotient, and nutrient deposition in veal calves during stages 2 and 3 (n = 32)

Item	Stage 2				Stage 3				SEM	<i>P</i> -value			
	F76 ¹	F88 ¹	F100 ¹	F112 ¹	F76	F88	F100	F112		Stage	Diet	Week	Diet × stage
Energy balance, kJ/kg of BW ^{0.85} per day													
ME intake	630	588	610	617	538	526	519	532	9	<0.01	0.12	0.25	0.51
Heat production ²													
As FHP	299	303	297	321	275	272	267	275	4	<0.01	0.46	0.66	0.74
As AHP	54	48	53	54	45	53	55	49	2	0.67	0.84	0.45	0.59
As TEF	49	48	51	34	36	42	46	47	2	0.51	0.57	0.29	0.17
Total	401	397	398	406	354	365	365	368	5	<0.01	0.79	0.14	0.85
Retained energy													
As protein	77	78	89	91	63	64	68	66	2	<0.01	0.14	0.33	0.59
As fat	153 ^a	113 ^{bc}	124 ^b	119 ^{bc}	122 ^{bc}	97 ^{cd}	86 ^d	98 ^{cd}	4	<0.01	<0.01	0.43	0.57
Total	230 ^a	191 ^{bcd}	213 ^{ab}	211 ^{abc}	184 ^{cde}	162 ^{ef}	154 ^f	164 ^{def}	5	<0.01	0.03	0.78	0.49
Adjusted ³	240	213	232	229	244	236	235	232	5	0.10	0.09	0.14	0.34
Respiratory quotient	0.93	0.93	0.93	0.92	0.93	0.92	0.92	0.92	0.002	0.82	0.42	0.81	0.86
Nutrient deposition, g/d													
Protein	205	215	247	253	247	257	275	268	6	<0.01	0.06	0.97	0.76
Lipid	243 ^{ab}	186 ^b	208 ^b	199 ^b	286 ^a	233 ^{ab}	212 ^b	235 ^{ab}	9	0.03	0.03	0.11	0.68
BW gain composition, /kg of gain													
Protein, g	177	173	162	174	171	195	180	186	3	0.15	0.65	0.99	0.58
Lipid, g	208 ^a	149 ^{cd}	135 ^d	138 ^{cd}	199 ^{ab}	177 ^{abc}	137 ^d	163 ^{bcd}	7	0.23	<0.01	0.06	0.45
Energy, MJ	12.4 ^a	10.0 ^{bc}	9.2 ^c	9.6 ^c	11.9 ^a	11.6 ^{ab}	9.7 ^c	10.9 ^{abc}	0.3	0.09	<0.01	0.14	0.30

^{a-f}Least squares means within a row with different superscripts differ ($P < 0.05$).

¹Crude protein concentrations in diets: F76 = 151 g/kg of DM; F88 = 174 g/kg of DM; F100 = 196 g/kg of DM; F112 = 221 g/kg of DM.

²FHP = fasting heat production; AHP = activity heat production; TEF = thermic effect of feeding.

³Retained energy was adjusted for the same ME intake (672 and 611 kJ/kg of BW^{0.85} per day for stages 2 and 3, respectively) and AHP (57 and 52 kJ/kg of BW^{0.85} per day for stages 2 and 3, respectively).

Figure 1. Relationship between N retention (RN) and digestible N intake (DN) in veal calves at 3 stages of fattening: □, stage 1; ■, stage 2; ○, stage 3; ●, data from Labussière et al. (2008). ^{a,b; A,B}Parameters of the regression with different superscripts differ ($P < 0.05$). Probability of equality of coefficient to 0: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ing stage 1 whatever the dietary CP content but was decreased below 75% with diets F100 and F112 during stage 2 and with diets F88, F100, and F112 during stage 3, indicating that DN allowance with these diets was greater than requirements of the calves.

The marginal efficiency of DN retention has been estimated as the slope of the linear regression between DN and RN. The relationship during stage 1 was linear, and the marginal efficiency of DN retention equaled 64% (Figure 1). This value is greater than that reported by Donnelly and Hutton (1976a; 45%) but similar to the value reported by Blome et al. (2003; 66%). Moreover, the gross efficiency of DN utilization did not significantly decrease with increasing dietary CP content during stage 1 as reported by Bartlett et al. (2006). The maximal DN allowance (1.77 g/MJ of ME) was therefore insufficient to satisfy maximum potential of the animal for RN and theoretical N requirements

(increasing from 40 to 48 g of DN/d between diets G76 and G112, NRC, 2001). The dietary CP content was then further increased in another experiment carried out during stage 1 using 120% of the reference CP concentration or 24.6% CP (Labussière et al., 2008, Figure 1) in calves of similar BW and ME intakes. The measured gross efficiency of RN remained high (72%), and DN allowance could therefore be increased up to 1.88 g/MJ of ME, which is lower than the value calculated from data of Bartlett et al. (2006; 2 g/MJ of ME). During stage 2, the linear relationship between DN and RN results to a marginal efficiency of DN retention equaling 40%, which is consistent with that estimated by Gerrits et al. (1996) in heavy calves. When testing a linear-plateau relationship to fit data from stage 2, slope in the ascending phase was therefore increased up to 56%, but residual standard error was twice the value in case of a linear relationship. There was no statistical

Table 9. Prediction equations for determining N requirements in veal calves

Item	n	Residual SD	R ²
DN ¹ (g/kg of DMI) = -2.5** (SE = 0.7) + 1.00*** (SE = 0.02) × NI (g/kg of DMI)	48	0.7	0.98
RN (g/kg of BW ^{0.85} per day) = -0.07 (SE = 0.06) + 0.81*** (SE = 0.07) × DN (g/kg of BW ^{0.85} per day)	26 ²	0.03	0.86
RN (g/d) = 28.3 (SE = 0.4) × BW gain (kg/d)	48	4.0	0.99 ³

¹DN = digestible N; NI = N intake; RN = retained N.

²Only the data from calves receiving N amounts below their theoretical N requirements (calculated according to NRC, 2001) were considered in the model for estimating metabolic urinary N. The effect of stage of fattening was not significant.

³Because no intercept was specified in the model, R² was redefined as 1 - sum of squares of error (model without intercept)/total sum of squares (model with intercept).

** $P < 0.01$; *** $P < 0.001$.

difference in RN between diets during stages 2 and 3. It can nevertheless be noted that RN during stage 2 was numerically greater with diet F100 than with diets F76 or F88, whereas there was a negligible increase in RN between diets F100 and F112. This may indicate that N requirements are probably satisfied with diet F100 during stage 2, which provided 1.51 g of DN/MJ of ME. During stage 3, there was no difference in RN between dietary CP concentration. Consequently, marginal efficiency of DN retention was low and equaled 18%, which is largely lower than the values reported by Gerrits et al. (1996; less than 30%). This has to be related to the decrease in gross efficiency of utilizing DN (from 66.0 to 49.5% during stage 3) according to results reported by Gerrits et al. (1996). During this stage, a DN allowance of 1.20 g/MJ of ME (corresponding to a F76 diet) may probably satisfy N requirements of the calves. Nevertheless, the latter value has to be considered cautiously, because variation of RN response to DN allowance increased as animals got older (Figure 1), which may decrease the precision of requirement estimation.

Several explanations have been put forward to explain the decrease in marginal efficiency of DN retention (van den Borne et al., 2006a). First, DN intake may have exceeded N requirements (70 g of DN/d, NRC, 2001) for all dietary CP concentrations (except F76 during stage 3), thereby affecting marginal N retention. Second, a lactose-induced insulin resistance may develop as the calf gets older (Hostettler-Allen et al., 1994), which can depress the ability of cells to uptake the extra nutrient supply out of the blood and therefore induce a low efficiency of protein utilization as animals get older. This assumption is also confirmed by the urinary glucose excretion that increased in the present trial from 8 g/d at stage 1 to 78 and 125 g/d at stages 2 and 3 (average over dietary CP contents; results not presented).

The maximum N gain increased with age from 32.8 to 40.5 and 44.0 g/d during stage 1, 2, and 3, respectively. Our data suggests that this maximum is below the potential N gain at stage 1, because daily RN could be further increased up to 35.0 g/d (average value for 4 calves receiving a 246 g of CP/kg of DM diet, Labussière et al., 2008, Figure 1). Diaz et al. (2001) observed N gains between 50 and 60 g/d with 65-to 105-kg male Holstein calves that received a 30% greater energy supply (900 vs. 672 kJ of ME/kg of BW^{0.85} per day). In conclusion, it appears that the N requirement for growth is very high in young veal calves (stage 1), allowing for a further increase in CP content of milk replacers; further investigation would be performed to assess if DN allowance should be further increased up to 1.88 g of DN/MJ of ME.

Utilization of Dietary Energy

The metabolizability of DE decreased numerically from 97% at stage 1 to 94% at stage 2 and 93% at stage 3 due to increasing energy losses in the urine (Tables 3 and 6). Data concerning stage 1 are in agreement with those of Diaz et al. (2001) but are greater than those of Blome et al. (2003). Nevertheless, the values for stages 2 and 3 are slightly lower than those measured by Gerrits et al. (1996) with calves of similar BW (120 kg, ME:DE = 96.5%; 200 kg, ME:DE = 95.3%). On average for all treatments, our calves were nevertheless fed greater amounts of DN, and they may have excreted greater urinary N, thus decreasing the ratio ME:DE.

During stage 1, the fraction of energy retained as protein increased linearly from 36 to 55% as dietary CP increased, which is in agreement with results of Blome et al. (2003) and Bartlett et al. (2006). During stages 2 and 3, the composition of retained energy differed between diet F76 and the other diets (67 vs. 55% as fat). The partitioning of energy between protein and lipid differed also between stages. Up to 55% of total energy was retained as protein during stage 1, whereas this was less than 45% for stages 2 and 3. Similar results were obtained by Vermorel et al. (1974). These results are consistent with the numerical reduction in respiratory quotient with age, indicating that increasing quantities of absorbed N are catabolized as animals get older (Gerrits et al., 1996).

Similar to results reported by Donnelly and Hut-ton (1976a), we did not observe an effect of dietary CP content on total HP, its components, or energy retention (Tables 5 and 8). Nevertheless, dietary CP affected differently the partitioning of energy retention between protein and lipid according to the stages. Previous work in growing pigs indicated that the gross efficiency of using ME differed for different nutrients (van Milgen et al., 2001) and body tissue deposition (protein vs. fat, Noblet et al., 1999). In our experiment, the substitution of fat and lactose for protein was not associated with variations in HP. Moreover, variations in dietary CP contents caused variations in the lipid deposition and in the fat content of BW gain. These variations were not associated with variations in HP: daily digestible fat intake was more than twice greater than the fat deposition in calves. Consequently, calves would deposit dietary fatty acids directly as body fat, which is associated with a low energy cost of deposition (van den Borne et al., 2007).

Growth Performance and Composition of BW Gain

During stage 1, the increased dietary CP content resulted in a numerical increase in BW gain, which agrees

with previous studies (Blome et al., 2003; Bartlett et al., 2006). In agreement with Gerrits et al. (1996), the BW gain was affected by dietary CP concentration during stage 2, whereas there was no effect during stage 3. The difference in response between stages may be partly explained by the relatively narrow range in dietary CP. It can also be argued that BW gain is estimated with a low precision ($SEM = 0.03$ kg) due to the short duration of measurement and the small number of animals per treatment.

In agreement with results of others (Diaz et al., 2001; Bartlett et al., 2006), the protein content of BW gain increased from 154 to 188 g/kg gain during stage 1 between diet G76 and the 3 other diets. The former could be explained by the low N supply, which could have limited protein deposition, or by the greater fat deposition, which may have diluted protein content in BW gain. The latter was greater than the value obtained from the relationship between RN and BW gain (177 g/kg of BW gain). It was also greater than the values obtained with male Holstein calves receiving diets with similar or greater CP contents (Tikofsky et al., 2001), but the latter were obtained using the comparative slaughter technique, and the balance technique used in the present experiment may have overestimated RN (Toullec et al., 1978). During stages 2 and 3, the protein content of BW gain averaged 170 and 183 g/kg of BW gain, respectively. These values are lower than those measured in veal calves weighing 145 to 187 kg and receiving similar amounts of ME and N (214 g/kg of BW gain; Vermorel et al., 1974) but greater than those calculated from the results of Gerrits et al. (1996; 155 to 175 g/kg of BW gain).

During stage 1, the lipid content of BW gain decreased with increasing dietary CP content, and it notably decreased for diet G112. The latter (90 g/kg of BW gain) is markedly lower than values measured in male calves of similar BW and for a similar dietary CP concentration (184 g/kg of BW gain; Donnelly and Hutton, 1976b; 129 g/kg of BW gain; Bartlett et al., 2006), but it is consistent with values measured by Blome et al. (2003; 87 g/kg of BW gain) with male Holstein calves. As suggested earlier by Diaz et al. (2001), the quantity of energy offered with diet G112 (and perhaps also with diet G120; Labussière et al., 2008) may not have been sufficient to ensure maximum fat deposition and BW gain. During stage 2, there was no effect of dietary CP content on the lipid content of BW gain between diets F88 and F112: only diet F76 resulted in a greater value for lipid concentration. During stage 3, lipid content of BW gain was lower with diet F100, and this may be partly due to the lower ME intake. These values are lower than those measured by Vermorel et al. (1974) with male calves of the Normande breed, but they are

in the range of values reported by Meulenbroeks et al. (1986) with Dutch Friesian and Holstein Friesian crossbred male calves (125 to 203 g/kg of BW gain).

CONCLUSIONS

The protein and fat deposition in veal calves was affected by the dietary CP concentration and mainly when calves were young. The effect of dietary CP on protein deposition was less pronounced or even negligible as calves got older, resulting in a low marginal efficiency of N utilization. The endogenous fecal N excretion was estimated as 2.5 g/kg of DMI per day, whereas metabolic urinary (maintenance) N was 0.07 g/kg of $BW^{0.85}$ per day. The N content of BW gain averaged 28 g/kg. These values can be used in the calculation of the N requirement of veal calves over their entire fattening period.

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