

Original article

Digestive capacity of the rabbit during the post-weaning period, according to the milk/solid feed intake pattern before weaning

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(Received 15 January 1999; accepted 17 May 1999)

Abstract — The milk/solid feed intake pattern and digestive capacity were compared in two groups of young rabbits reared between 16 and 32 days in litters of four (L4 group, $n = 18$ litters) or ten pups (L10, $n = 20$) in order to modulate milk availability. Compared to the L4 group, rabbits in the L10 group presented a lower milk intake (22.3 versus 28.8 g·day $^{-1}$) and a higher solid feed intake (12.9 versus 8.0 g·day $^{-1}$) between 16 and 32 days of age. Live weight and weight gain were significantly lower in the L10 (-15%) than in the L4 group from 22 until 42 days. No significant difference was observed among the two groups for post-weaning digestibility and for the intraluminal specific or total activities of amylase and maltase. The total intraluminal activity (pool of enzyme) of amylase and maltase doubled between weaning (32 days) and 42 days. At weaning, the specific activity of amylase was similar in the jejunal and ileal segments (8.5 AU·g $^{-1}$). From 32 to 42 days, the specific amylase activity doubled in the jejunum, while it remained steady in the ileum. The intraluminal specific maltase activity did not significantly change between 32 and 42 days, while it was twice as high in the jejunum compared to the ileum (3.5 versus 1.8 μmoles hydrolysed maltose·g $^{-1}$, respectively). © Inra/Elsevier, Paris.

digestion / weaning / rabbit / amylase / maltase

Résumé — Capacité digestive du lapereau après sevrage, en fonction de l'ingestion lait/aliment avant le sevrage. Le profil d'ingestion (lait et aliment sec) ainsi que la capacité digestive ont été comparés sur deux groupes de lapereaux élevés, entre 16 et 32 j d'âge, en portées de dix (groupe L10, $n = 20$ portées) ou en portées de quatre petits (L4, $n = 20$), afin de moduler la disponibilité en lait. Par rapport au groupe L4, les lapereaux du groupe L10 présentent pendant la période 16–32 j, une plus faible ingestion de lait (22,3 vs 28,8 g·j $^{-1}$; figure 1), mais une consommation plus importante d'aliment solide (12,9 vs 8,0 g·j $^{-1}$). Parallèlement, les lapereaux du groupe L10 présentent dès 22 j d'âge un poids vif significativement inférieur (-15% , figure 2); cet écart étant maintenu jusqu'à 42 j d'âge, ces animaux ont donc une vitesse de croissance plus faible (24,6 vs 28,8 g·j $^{-1}$). Aucune différence

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significative de digestibilité fécale des nutriments n'a été mesurée entre les groupes L10 et L4 (*tableau II*). De même, l'activité intraluminale totale ou spécifique de l'amylase et de la maltase (*tableau III*) n'a pas montré d'écart significatif entre les deux groupes. L'activité totale intraluminale (pool enzymatique, calculé pour un segment intestinal) de l'amylase et de la maltase double entre le sevrage (32 j) et 42 j d'âge. L'activité spécifique amylasique est similaire à 32 j entre le jéjunum et l'iléon (8,5 AU·g⁻¹ contenu, *figure 3*). Durant les 2 semaines post-sevrage, l'activité spécifique amylasique double au niveau jéjunal, alors qu'elle demeure constante au niveau iléal. L'activité intraluminale spécifique de la maltase n'a pas varié significativement entre 32 et 42 j (en moyenne 2,6 µmoles maltose hydrolysé·g⁻¹ contenu frais·min⁻¹), mais sa valeur au niveau jéjunal est double de celle mesurée au niveau iléal (resp. 3,5 et 1,8). © Inra/Elsevier, Paris.

digestion / sevrage / lapin / amylase / maltase

1. INTRODUCTION

Digestive disorders, frequently observed in rabbit breeding during the weaning period (21–40 days of age) have been related to the intake pattern (quality and quantity) and maturation of the digestive process [17, 19]. More particularly, an incomplete intestinal digestion of starch, corresponding to an overflow of readily available carbohydrates entering the caecum, could alter microbial activity and could lead to digestive troubles [5, 16]. An earlier intake of solid feed may improve such maturation and may result in a decreased post-weaning mortality [24]. However, the effect of a change in the intake pattern on the maturation of digestive enzymes is only slightly documented [15]. For instance, the intake behaviour of the rabbit before weaning has mainly been documented for milk but not for solid feed [20, 26]. However, the maturation of enzyme secretion implicated in glucidic digestion, according to age and starch feed intake, have been mainly obtained for the pancreas [2, 7, 12, 13, 22]. But almost no information is known about amylase or maltase activity in the small intestine [6]. Moreover, the global digestive capacity that could be addressed through the pool of enzymes effectively active in the lumen has never been evaluated according to the feeding behaviour of the young rabbit.

Therefore, the aim of this work was to study how the suckling rabbit adapts its

feeding pattern (milk and solid feed) according to the availability of milk (modulated by litter size), and if that modulates its capacity to degrade dietary starch. In addition, we aimed at developing an original approach for the study of the glucidic digestive capacity of the rabbit around weaning, by evaluating the intestinal intraluminal (jejunum and ileum) pool of enzymes able to hydrolyse starch and maltose.

2. MATERIALS AND METHODS

2.1. Animals and feeding

To modulate the milk/feed intake pattern before weaning, 40 litters (with ten young per litter at birth, day 0) were submitted to a low or a high availability of milk, through a variation in litter size: on day 16, 20 litters were reduced to four pups per litter (L4 group), while the others were maintained at ten (L10 group). Litters were obtained from primiparous hybrid females (strain Inra A1066 × A1077). Live weight and milk intake of suckling rabbits were measured individually at 16, 22, 25, 29 and 32 days of age.

To measure the solid feed intake of the litters without separating the young from their mothers, cages were equipped with wired separations (on day 16) allowing only the passage of the young, thus creating a space reserved for them. From day 16 until weaning (day 32) a maternal commercial feed (*table I*) was distributed ad libitum to the young in specific feeders (special shape, location in part reserved to the young), and to the females in feeders not accessible to the young. Solid feed intake was measured every

Table I. Ingredients and chemical composition of feeds given to females and litters, or to growing rabbits after weaning.

Diets	Females and litters‡	Growing rabbits
Ingredients		
Barley		10.00
Wheat		10.00
Soybean meal		6.00
Sunflower meal		12.00
Lucerne meal		25.00
Dehydrated beet pulp		10.00
Wheat bran		20.35
Beet molasses		5.00
CMV*		1.65
Chemical composition (% DM)		
Organic matter	90.1	91.6
Crude protein (N*6.25)	19.2	19.7
Starch	14.2	19.1
NNCC**	36.6	40.1
NDF	34.3	31.8
ADF	17.7	18.3
ADL	4.3	4.6

* Bicalcium phosphate -0.10 %; calcium carbonate -0.30 %; minerals, vitamins and salt -1.00 %; DL₄₀ Methionine -0.25 %; Robenidine (66 ppm).

** Non-nitrogenous cellular content (OM-NDF-CP).

‡ Commercial feed, proximate ingredients composition (cereals 11 %, vegetable protein source 30 %, fibre source 52 %, molasses 4 %, minerals and vitamins 4 %).

2 days from 16 days of age until weaning and then at 39 and 42 days of age. After weaning, rabbits were kept in individual cages, and they were fed experimental diets meeting recent nutritional recommendations, ad libitum (for description, see *table I*) [10].

2.2. Digestibility measurements and collection of intestinal content

Digestibility measurements were performed on two groups of 12 rabbits each (L4, L10) kept in individual metabolism cages. After a 10-day adaptation period (32–42 days old), the apparent digestibility coefficients were calculated from the total collection of faeces for four consecutive days (European reference method [14]). Faeces were pooled individually in plastic bags and stored at -18 °C until subsequent analyses.

The intraluminal enzymatic activities were measured from samples of the jejunum and ileum

(20 cm) obtained from rabbits killed by cervical dislocation at 32 and 42 days of age, between 10.00 and 12.00 hours. After laparotomy, the digestive tract was withdrawn and the jejunal segment was identified and clamped 5 cm after the Treitz loop and 20 cm further on. Similarly, the terminal ileal segment was clamped at 25 and 5 cm before the ileo-caecal junction. The luminal content of the segment was then sampled by slight manual pressure, directly in a centrifugal tube maintained in ice. The overall sampling procedure did not exceed 10 min. The tubes were then weighed and frozen at -80 °C until further processing.

2.3. Analytical procedures

Dry matter (DM) was determined on duplicate samples by heating at 103 °C for 24 h. Organic matter (OM) was determined by ashing at 550 °C for 5 h. Nitrogen was determined

according to the Dumas procedure (autoanalyseur LECO, mod. FP428). Starch was hydrolysed enzymatically and the resultant glucose was measured by using the hexokinase (EC 2.7.1.1) glucose-6-phosphate dehydrogenase (NAD) (EC 1.1.1.49) system (Boehringer, Mannheim). Gross energy was measured with an adiabatic bomb calorimeter (PARR, Moline, IL). Acid detergent fibre (ADF), acid detergent lignin (ADL) and neutral detergent fibre (NDF) were determined according to the sequential procedure of Van Soest et al. [31]. In order to evaluate the overall content in readily available carbohydrates (starch, oligosaccharides, free saccharides, etc.), the non-nitrogenous cellular content was calculated as the difference between OM and CP and NDF.

After defrosting, samples of the intraluminal intestinal content (1–2 g) were diluted with 5 mL of a physiological solution (9 g NaCl·L⁻¹) and then homogenised (Ultra-Turrax, 8 000 tr·min⁻¹) and centrifuged (15 min, +3 °C, 5 000 g). The supernatant was frozen at -80 °C until subsequent analyses. Amylase activity was determined according to the procedure of Corring and Saucier [7], and was expressed as the amylolytic activity unit 'AU'·min⁻¹·g⁻¹ fresh content (specific activity) or per gram total segment collected (total activity). AU was the quantity of enzyme which hydrolysed 1 mg of starch at 37 °C. The maltase activity was determined according to the procedure of Dahlqvist [9], and was expressed in µmoles hydrolysed maltose·min⁻¹·g⁻¹ fresh content (specific activity) or per total segment collected (total activity). Following Shields et al. [29] and Kelly et al. [18], we adopted two types of expression. Specific activity was considered as a qualitative indicator of the intraluminal potential of hydrolysis of a substrate. Total activity corresponded to the pool of enzyme activity present in a segment, and could be assimilated to the intestinal hydrolysing capacity of a substrate.

2.4. Statistical analyses

The results were subjected to analysis of variance according to the general linear model procedure of the Statistical Analysis System [28]. Data for enzyme activity were analysed according to a three factorial model (age, site, litter size) with corresponding interactions. Interactions between site and litter, as well as between age and litter were found to be non-significant ($P > 0.20$) and are not presented in *table III*.

3. RESULTS

3.1. Feed intake pattern, growth and faecal digestibility

The weights of the young rabbits at birth (50.8 g) and on day 16 (199.4 g) as well as their milk intake on day 16 were similar in both groups. Between 16 and 32 days of age (weaning), the individual milk intake was 23 % higher for the L4 than for the L10 group (460 g versus 357 g; $P < 0.05$). This difference was more pronounced between days 20 and 26 of lactation (*figure 1*). A very weak feed intake was registered before day 20 (mean $< 2 \text{ g} \cdot \text{d}^{-1} \cdot \text{rabbit}^{-1}$). On day 21, however, rabbits ate more than $2.5 \text{ g} \cdot \text{d}^{-1} \cdot \text{rabbit}^{-1}$ in ten of the 20 litters in group L10, compared to two of 18 litters in group L4. From day 16 until weaning, the solid feed intake was 62 % higher in the L10 group than in the L4 group (207 versus 128 g, $P < 0.01$). Nevertheless, rabbits gained more weight between days 16 and 32 (*figure 2*) in the L4 than in the L10 group (461 g versus 394 g, $P < 0.05$). Rabbits of the L4 group reached a higher (+10 %) weight at weaning (661 g versus 595 g, $P < 0.01$), and maintained a higher live weight until 42 days of age (1 084 g versus 979 g, $P < 0.01$). The post-weaning (32–42 days) weight gain was, however, only slightly higher in the L4, compared to the L10 group (38.9 and 35.1 g·d⁻¹, $P = 0.08$, respectively).

The digestibility in the whole tract was not significantly different among the two groups, whatever the nutrient concerned (*table II*). The nutritive value of the experimental feed was in accordance with initial formulation objectives: digestible energy 'DE' = 12.65 MJ·kg⁻¹ DM; digestible protein 'DP' = 154 g·kg⁻¹ DM; and the ratio DP/DE = 11.7 g DP/MJ ED.

3.2. Intraluminal amylolytic and maltasic activity

The specific or total amylase and maltase activities did not differ significantly

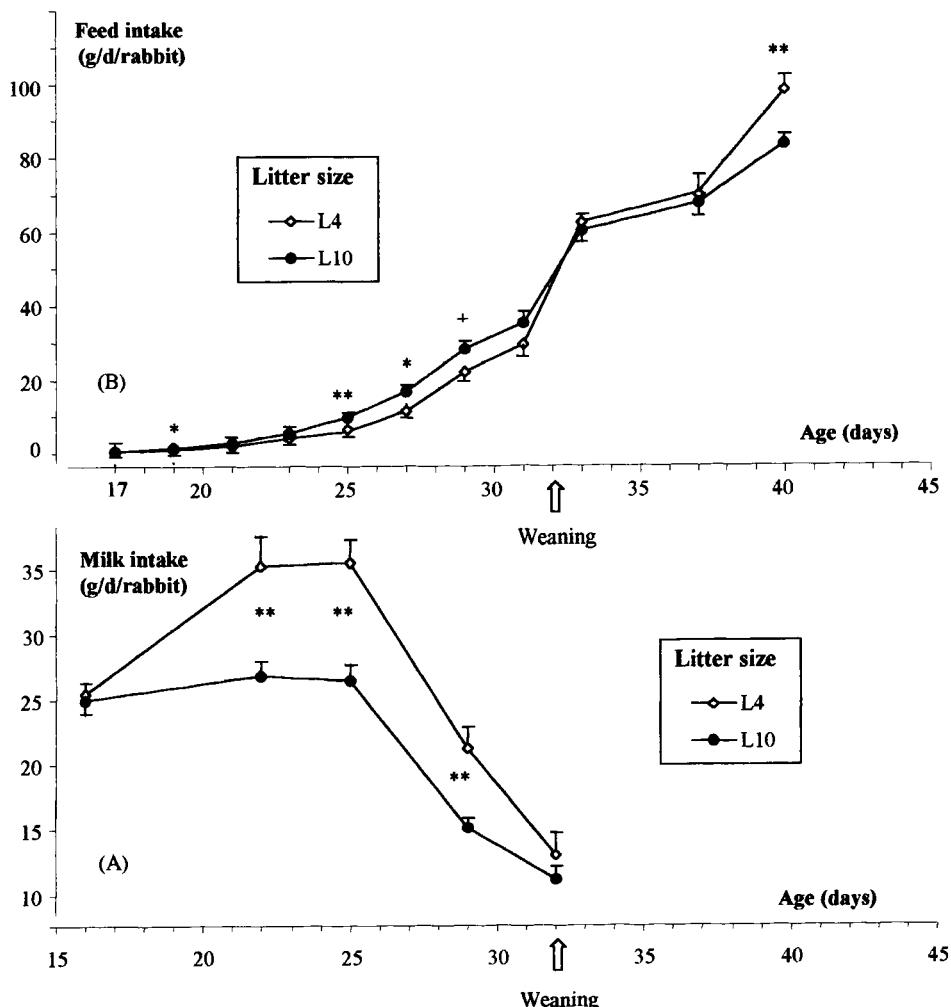


Figure 1. Milk (A) and solid feed intake (B) from 16 to 42 days of age, according to litter size (four pups: L4; ten pups: L10) before weaning (32 days). Values are means \pm standard error of the mean (SEM). Within age, means differed significantly at the level $P < 0.01$ (**), $P < 0.05$ (*), $P < 0.1$ (+).

among the L4 or L10 groups (*table III*). A significant interaction between age and site ($P < 0.01$) was observed for the specific amylase activity (*table III*). Between 32 and 42 days of age, the activity doubled in the jejunum, while it remained steady in the ileum (mean $8.5 \text{ AU} \cdot \text{g}^{-1}$ content, *figure 3*). A similar specific activity of maltase was

observed for 32- or 42-day-old rabbits, but was twice as high in the jejunum than in the ileum segment ($P < 0.01$).

When expressed as total activity (*table III*), the pool of amylase and maltase almost doubled (in the jejunum and ileum, $P < 0.01$) between 32 and 42 days of age. With respect to the intestinal segment, the total activity of

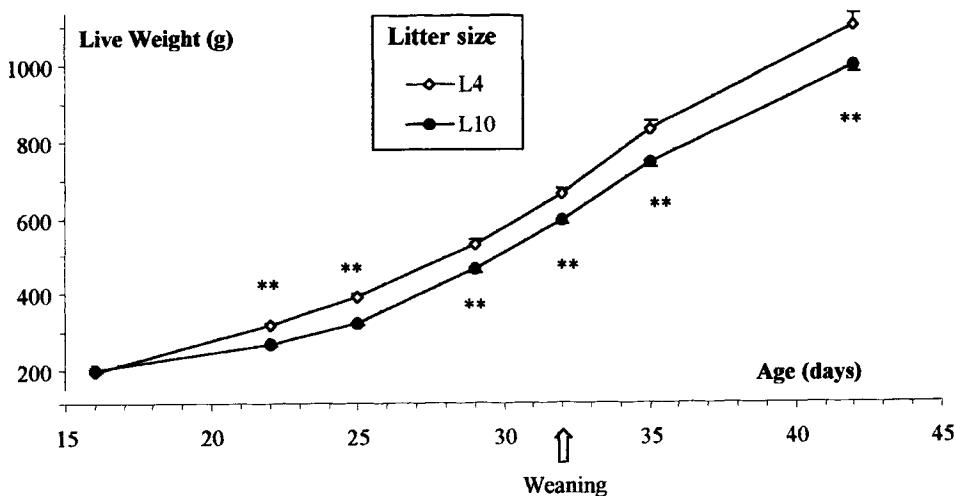


Figure 2. Growth of rabbits from 16 to 42 days of age, according to litter size (four pups: L4; ten pups: L10) before weaning (32 days). Values are means \pm standard error of the mean (SEM). Within age, means differed significantly at the level $P < 0.01$ (**).

Table II. Whole tract digestibility of experimental feed (growing), measured on 42-day-old rabbits previously maintained in litters of four (L4) or ten (L10).

Litter size	L4	L10	SEM	Pr > F
Digestibility coefficients (%)				
Organic matter	70.8	70.1	0.46	0.28
NNCC*	95.7	95.6	0.28	0.93
Energy	69.4	68.6	0.47	0.30
Crude protein	78.7	77.1	0.66	0.11
NDF	34.5	33.4	0.91	0.41

* Non-nitrogenous cellular content (OM-NDF-CP)

4. DISCUSSION

Until the age of 16 days, the rabbit exclusively consumed milk, and began to eat some pellets of solid feed between 18 and 20 days of age (a mean of $2 \text{ g} \cdot \text{day}^{-1} \cdot \text{rabbit}^{-1}$). A previous report [24] mentioned no significant pellet intake before the age of 22–23 days. Unfortunately, because the young must be reared in litters, we could not measure the individual solid feed intake, and we were therefore not able to estimate the interindividual variability. In agreement with the results of De Blas et al. [11], the total mean solid feed intake before weaning was $170 \text{ g} \cdot \text{rabbit}^{-1}$. But it increased by 38 % in the litters of ten while their milk intake was 22 % lower than in the litters of four. These results suggested that under competition for milk intake, the beginning of solid feed intake occurred earlier and the feed/milk intake ratio was higher. Furthermore, considering that the mean DM level of milk between days 16 and 32 of lactation is 32 % [21, 27], the total DM intake (milk + pellets) for rabbits reared in litters of ten

maltase and amylase also doubled between the jejunum and the ileum. Obviously, it was related to an increase in the intraluminal fresh content, which doubled for the ileum (3.46 g versus 7.11 g, $P < 0.01$) while it increased by only 32 % for the jejunum (1.23 g versus 1.81 g, $P < 0.10$).

Table III. Intraluminal amylolytic and maltasic activity, according to age, digestive site and litter size, in the weaning rabbit.

	Age		Digestive site		Pr > F		
	32 days	42 days	Jejunum	Ileum	SEM	Age	Site
							litter size
Specific activity (per gram fresh content)							
Amylase*	8.46	12.40	11.17	9.81	1.07	< 0.01	0.46
Maltase **	2.72	2.43	3.49	1.76	0.66	0.60	< 0.01
Total activity (per segment)	24.61	48.68	19.25	55.19	9.34	< 0.01	0.74
Amylase*	4.60	8.81	4.90	8.70	1.33	< 0.01	0.010
Maltase **	2.41	4.70	1.71	5.62	0.67	< 0.01	0.14
Luminal content (g)							< 0.01

* Expressed as AU·min⁻¹·g⁻¹ content or per total segment. AU is the quantity of enzyme which hydrolyses 1 mg of starch·min⁻¹.

** Expressed in µmoles maltose hydrolysed·min⁻¹·g⁻¹ fresh content or per total segment.

[†] Other interactions (site × litter and age × litter) are not significant ($P > 0.20$).

SEM: standard error of the mean (pooled data among L4 and L10 group).

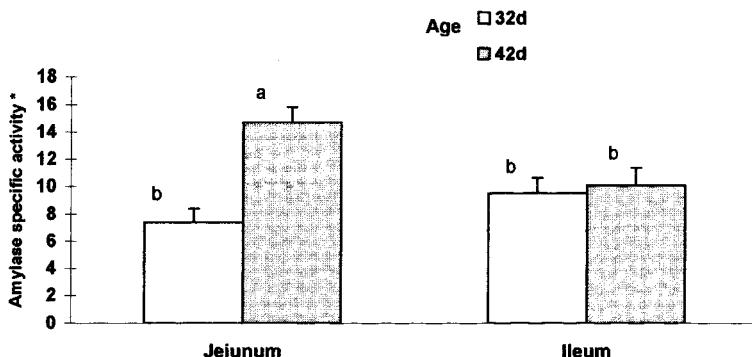


Figure 3. Intraluminal amylolytic specific activity, according to age and digestive site. * Mean values (\pm SEM), expressed as the amylasic unit 'AU'·min $^{-1}$ ·g $^{-1}$ fresh content. a, b: means having a common superscript letter did not significantly differ at $P < 0.05$.

was 14 % higher than those raised in litters of four (300 and 262 g DM for the 16–32-day period, respectively). This compensatory effect of pellet intake was not, however, sufficient to ensure a post-weaning growth similar to that of rabbits kept in a litter of four. These results were in agreement with McNitt and Moody [26], who reported a higher weaning weight and growth during the post-weaning period, when the pups consumed more milk during lactation.

This modulation in the milk/solid feed intake ratio did not seem to affect the overall post-weaning feed digestion. More particularly, the degradation of the glucidic fraction (NNCC, mainly starch and simple saccharides) in the whole tract (intestinal + microbial digestion) was almost complete as previously reported [4, 11, 17]. Similarly, the feeding behaviour before weaning did not affect the post-weaning intestinal capacity to degrade starch or maltose, either estimated through the intraluminal (jejunum or ileum) specific or total activity of amylase or maltase. This was consistent with Corring et al. [7] who reported that the pancreatic amylase level was not affected by a shorter sucking period (until 21 days instead of 30 days, without dry feed).

The digestive capacity for starch hydrolysis, estimated by measuring the amylase

and maltase total intraluminal activities, doubled during the ten post-weaning days. Between weaning and 3 months of age, Marounek [25] also reported a three-fold increase in total intestinal amylolytic activity. Because the luminal content doubled as well, this suggested a four-fold increase in enzyme secretion from the pancreas and intestine. This sharp increase in the starch digestive capacity after weaning was also suggested by the measurements in the starch level in the ileal contents that decreased sharply during the two post-weaning weeks [4]. Besides the effect of age, we cannot exclude an effect of dietary starch by itself on amylase activity as classically observed in other species. However, it was only recently described in adult rabbits [1], and not for the growing rabbit [8]. During the ten post-weaning days, an increase in the enzymatic intraluminal specific activity was measured in the jejunum only for amylase, in agreement with Marounek [25]. The origin of this increase of the amylolytic activity remains unclear. Amylase is mainly secreted by the pancreas; however, in adult rabbits the secretion of amylase by the duodenal mucosa was also observed [6], but was ten times lower than pancreatic secretion [1]. Corring et al. [25] demonstrated the importance of ontogenetic factors compared to dietary factors on amylolytic pan-

creative activity around the weaning period. However, the results should be considered with caution, since the increase in pancreatic amylase varied greatly according to the authors between 15 and 43 days of age: 60 or 5 times or no variations ([2, 8, 13], respectively). Inversely, the specific intraluminal maltase activity did not change during the ten post-weaning days. This was consistent with the results of Toofanian [30], who reported an increase in maltasic activity of the intestinal mucosa only between 20 and 30 days of age, and no change after weaning. A similar trend was also observed in piglets [3, 23]. Therefore, the development of maltase activity would be mainly controlled by ontogenetic factors rather than by nutritional factors. We observed, however, a lower maltasic activity in the lumen of the ileum compared to the jejunum. This was in agreement with the results of Dojana et al. [13], obtained for the ileal and jejunal mucosa. This was also confirmed for the relationship between measurements of maltase in the lumen and in the mucosa of the small intestine.

In conclusion, a change in the milk/solid feed intake pattern before weaning did not lead to major changes in the post-weaning digestive capacity. We confirmed that starch digestion sharply increases during the two post-weaning weeks, although the specific maltase activity evolved independently of age. Further investigations are now necessary to specify the impact of nutrient intake before weaning (particularly the available carbohydrate/fibre ratio) on the digestive system development and nutrient digestibility.

ACKNOWLEDGEMENTS

The authors thank André Lapanouse, Jacques De Dapper and Muriel Sécura for their technical assistance (Station de recherches cunicoles, Inra Toulouse). This study was supported by a post-doctoral fellowship grant of CNPq (National Council for Scientific and Technological Development – Brazil), and by U.C.A.A.B. (Château-Thierry, France).

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