Reprod. Nutr. Dev. 40 (2000) 249–260

Original article

Age-related changes in apparent digestibility in growing kittens

E. Jean HARPER*, Catherine L. TURNER

WALTHAM Centre for Pet Nutrition, Freeby Lane, Waltham-on-the Wolds, Melton Mowbray, Leics, UK

(Received 13 September 1999; accepted 11 April 2000)

Abstract — The ability of the growing kitten to digest protein, fat, carbohydrate, dry-matter and energy were assessed. Kittens were divided into two groups; one group was fed a wet diet, the other a dry diet. Both groups were allowed ad libitum access to food. Apparent digestibility of the two diets, and kitten bodyweights were measured over a 24-week period. There were no significant differences in mean bodyweight between the two groups. Digestible energy intake of the kittens decreased with increased age; regression analysis of the data generated two fitted models which appeared to accurately predict the digestible energy intake between 39 and 41 weeks of age. There was a significant ($P < 0.05$) effect of diet on the apparent digestibility of protein, organic-matter and dry-matter. Age had a significant ($P < 0.05$) effect on the apparent digestibility of all the parameters measured. Newman-Keuls multiple range tests showed that apparent digestibility of carbohydrate, organic-matter and total energy significantly ($P < 0.05$) increased in kittens older than 19 weeks. This suggests that the digestive capacity of the younger cat may be affected by the physiological development of the gut, and dietary induced enzyme modulation.

kitten / digestibility / growing / diet / gut

Résumé — Évolution de la digestibilité apparente en fonction de l'âge chez des chats en croissance. La capacité à digérer les protéines, les graisses, les glucides, la matière sèche et l'énergie a été étudiée chez des chats en croissance. Deux groupes de chatons ont été constitués : un groupe nourri avec un aliment humide, l'autre avec un aliment sec. Les deux groupes ont eu accès ad libitum à l'aliment attribué. La digestibilité apparente des deux régimes et le poids des chats ont été mesurés pendant une période de 24 semaines. Le poids des deux groupes d'animaux n'a pas été significativement différent. La consommation en énergie digestible des chatons a diminué au fur et mesure que les chats ont grandi ; une analyse des données par régression a débouché sur deux modèles qui permettent de prédire de façon précise la consommation en énergie digestible de chats âgés de 39 à 41 semaines. Seules les digestibilités apparentes des protéines, de la matière organique et de la matière sèche ont été différentes entre les deux régimes ($P < 0,05$). L'âge a eu un effet significatif ($P < 0,05$) sur la digestibilité apparente de tous les paramètres mesurés. Le test statistique de Newman-Keuls a montré que la digestibilité apparente des carbohydrates, de la matière organique et

* Correspondence and reprints
E-mail: waltham.centre@eu.effem.com

de l'énergie totale augmente chez les chatons âgés de plus de 19 semaines (P < 0,05). Ceci permet de suggérer que la capacité digestive des chatons évolue avec le développement physiologique de l'intestin grêle et avec l'adaptation enzymatique induite par l'alimentation.

chat / digestibilité / croissance / aliment / alimentation

1. INTRODUCTION

A plethora of examples is contained within the literature, highlighting the importance of the marked adaptations of the gastro-intestinal (GI) tract required by the young mammal in the first days or months after birth that are so essential to its health and development. Most of these examples focus on the physiological and developmental changes which occur in the neonate and during the subsequent suckling period, but a few comment on changes which occur at weaning.

Previous studies have indicated greatly reduced digestive capacity in the younger cat [21, 25]. This is contrary to data described for the puppy, where digestibility does not appear to be affected by the physiological development of the intestine occurring during growth. Labrador Retriever puppies between twelve and twenty weeks of age showed good digestibilities of all nutrients with no statistically significant influence of age or diet [7]. Literature relating to digestibility in companion animals is minimal, and that in the kitten is almost non-existent. The aim of this study was to investigate changes in digestibility within weaned kittens and their subsequent juvenile growth period and to pinpoint the age at which digestive efficiency achieves normal adult levels.

2. MATERIALS AND METHODS

2.1. Kittens and diets

Twelve, eight-week old healthy kittens (six male, six female) representing four litters were randomly assigned to two commercial diets to give a similar male female split on each diet. Of the two diets one represented a wet product, the other a dry; both were nutritionally complete [3]. The macronutrient and ingredient compositions of the diets are shown in Table I.

Kittens were housed individually, but, socialised in groups of three under constant supervision. Kittens were given ad libitum access to food and fresh water. Daily food intakes and weekly bodyweight (BW) were recorded for each kitten. Assessment of apparent digestibility was performed for each kitten by a 14-day faeces collection at 9–11, 14–16, 19–21, 24–26, and 30–32 weeks of age. Food and faeces samples were analysed for proximate nutrients and energy (bomb calorimetry) to determine apparent digestibilities.

2.2. Methods for determining digestibility

Food intake was measured and the food composition analysed. Faeces from each kitten were stored frozen over a fourteen day collection period. The faeces collected within this period for an individual animal were pooled, and analysed for gross energy (bomb calorimetry), protein (Dumas method), fat (acid-ether extract), ash and moisture (thermogravimetric analysis). Apparent digestibility was calculated using the equation: *(Intake – Output)/Intake*.

2.3. Statistical analysis

All data were available and were analysed using a balanced nested ANOVA procedure from Minitab version 10.1. The model included the effect of kitten,

Table I. Macronutrient and ingredient profile of diets of the kittens.

Diet type	Macronutrient profile		Ingredient profile	
	Macronutrient	Composition ($g \cdot 400\ kcal^{-1}$)	Ingredient	Composition ($g \cdot 100\ g^{-1}$ DM)
Wet	Protein	44.6	Meat and animal derivatives from:	
	Fat	20.2	Poultry	33.8
	Carbohydrate	32.4	Pork	30.8
	Ash	12.2	Beef	20.4
			Wheat flour	14.0
			Vitamin and mineral mix	1.0
Dry	Protein	39.7	Cereals:	
	Fat	13.5	Corn	21.26
	Carbohydrate	49.0	Rice	16.5
	Ash	8.4	Wheat	11.0
			Meat and animal derivatives from:	
			Poultry	31.9
			Corn gluten meal	12.8
			Beef tallow	3.5
			Milk and milk derivatives	2.0
			Vitamin and mineral mix	1.0

Kittens were offered food ad libitum.

age-range and diet, and kitten nested within diet was considered as the error term for testing the diet effect. The interaction between age-range and diet was also examined. The model used for testing BW was similar to that for testing digestibility with the exception that age points were used rather than an age-range. Differences were considered significant at $P < 0.05$. Digestibility parameters showing significant differences for age were further analysed using Newman-Keuls multiple range test using the method described in Hicks [9]. Digestible energy intake models were predicted using the regression analysis procedure from Statgraphics plus version 2.1. All means are quoted ± standard deviation (SD) unless otherwise stated.

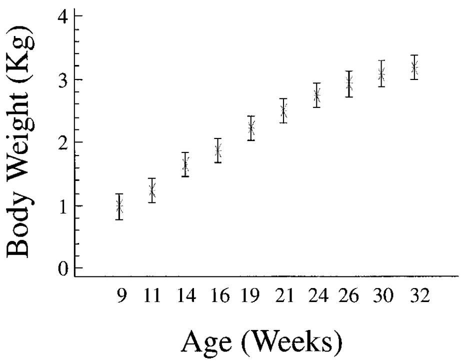

Figure 1. Mean growth curve ± 95% least significant difference of the kittens over the trial period. Mean body-weight (kg) was calculated irrespective of diet group (n = 12) and is plotted with age (weeks). There was no significant difference between diet and bodyweight.

3. RESULTS

No significant difference in BW or weight-gain was found between the two groups of kittens. The mean growth curve during the test period is shown in Figure 1. Average BW gain during the trial period is shown in Table II. Change in body weight

Table II. Mean apparent digestibility coefficient and mean body weight gain ± SD with age range (weeks). Digestibility coefficients and bodyweight gains were calculated from the total number of kittens used in the study, irrespective of diet group: $n = 12$.

Digestibility parameter	Age-range weeks				
	9–11	14–16	19–21	24–26	30–32
Organic matter	0.84 ± 0.03[a]	0.85 ± 0.03[a]	0.88 ± 0.02[b]	0.87 ± 0.02[b]	0.88 ± 0.02[b]
Dry matter	0.82 ± 0.03[a]	0.82 ± 0.03[ab]	0.85 ± 0.02[b]	0.84 ± 0.02[ab]	0.84 ± 0.03[ab]
Protein	0.83 ± 0.04[a]	0.84 ± 0.04[ab]	0.86 ± 0.03[b]	0.85 ± 0.02[b]	0.85 ± 0.03[b]
Energy	0.83 ± 0.04[a]	0.85 ± 0.03[a]	0.88 ± 0.02[b]	0.87 ± 0.02[b]	0.87 ± 0.02[b]
Fat	0.86 ± 0.04[a]	0.89 ± 0.08[ab]	0.90 ± 0.08[ab]	0.92 ± 0.02[b]	0.92 ± 0.03[b]
Carbohydrate	0.85 ± 0.03[a]	0.85 ± 0.03[a]	0.88 ± 0.02[b]	0.88 ± 0.02[b]	0.88 ± 0.02[b]
Mean body weight gain (g)	261.9 ± 52.78[a]	215.4 ± 100.37[a]	262.17 ± 121.85[a]	230.67 ± 78.67[a]	17.58 ± 70.11[b]
DE intake $kJ.kg^{-1}$ BW/14day period[c]	11 935 ± 1 502	8 641 ± 1 276	7 640 ± 878	6 978 ± 1 028	5 291 ± 654

[a, b] Newman-Keuls homogeneous groupings for a parameter, calculated using the method from Hicks [9].
[c] Digestible energy (DE) intakes are calculated for 14 day periods corresponding to age-ranges.

significantly ($P < 0.05$) differed with age. A Newman-Keuls multiple range test showed the mean change in BW between 30 and 32 weeks to be significantly ($P < 0.05$) lower than preceding changes. There was no significant difference in mean BW changes between weeks nine and 26. The average body weight gain of the twelve kittens over the total trial period was 2.20 ± 0.74 kg.

Digestible energy (DE) intake decreased on a BW basis with increasing age (Tab. II). Between 30 and 32-weeks of age DE intake was 5291.13 ± 654.29 $kJ \cdot kg^{-1}$ BW; an average of 370 $kJ \cdot kg^{-1}$ $BW \cdot d^{-1}$. The NRC recommended daily intake of DE of the active adult cat is 334 $kJ \cdot kg^{-1}$ $BW \cdot d^{-1}$ [22].

DE intake of the fully grown kittens was calculated from the data shown in Table II. Regression analysis gives seven models with an R-squared value greater than 75%. Of these, the three with the smallest residual errors were chosen to forecast the DE intake of the fully grown kittens. The models predict a daily DE intake on a BW (kg) basis of between 235 and 308 kJ (Tab. III).

Tables II and IV show component digestibilities with diet and kitten age. Apparent digestible energy was not significantly different between diet, neither were mean apparent digestibility coefficients for fat or carbohydrate. Mean apparent digestibility coefficients for dry-matter, organic-matter and protein were significantly different ($P < 0.05$). In each case, the apparent digestibility of the dry food was higher than the wet. Mean apparent digestibility coefficients between diet for dry-matter, organic-matter and protein were all within the range 0.821 to 0.872 (Tab. IV).

Apparent digestibility of all parameters measured, significantly ($P < 0.05$) varied with kitten age. Generally, digestibility appeared to increase with age to a maximum between 19 and 21 weeks, and then started to decline. However, in all cases, there was no significant difference between the digestibility at the 19–21 week peak and the subsequent age periods (Tab. II).

Newman-Keuls multiple range tests showed mean apparent digestibility of carbohydrate, organic-matter and energy to fall

Table III. Fitted models describing the relationship between digestible energy intake and catagorised age-range.

Model	Equation of the fitted model	R^2 value (%)	Residual error[a]	Calculated daily DE intake[b]
Logarithmic – X	DE intake (14 days) = 11 767.3 – 3 833.26 × ln age-range[c]	79.2	1.29×10^{-6}	307.7
Square root – X	DE intake (14 days) = 16 409.0 – 4 958.03 × $\sqrt{\text{age-range}^{c}}$	77.6	1.39×10^{-6}	235.1
Reciprocal – Y	DE intake (14 days) = $1/(6.20458 \times 10^{-5} + 2.422 \times 10^{-5} \times \text{age-range}^{c})$	75.2	4.0×10^{-10}	308.0

[a] The residual mean square error.
[b] Digestible energy (DE) intake calculated in $kJ \cdot kg^{-1}$ $BW \cdot d^{-1}$.
[c] As it is impossible to multiply by a range, each age-range was categorised by a *number* which ascended with increasing age-range. Age-range 9–11 weeks was given number 1; 14–16 weeks number 2, and so on. The calculated number for an age range 39-41 weeks was 7. Using the reciprocal-Y model, the calculated digestible energy intake between 39 and 41 weeks is 4 319.05 $kJ \cdot kg^{-1}$ BW over a 14 day period, or an average digestible energy intake of 308 $kJ \cdot kg^{-1}$ $BW \cdot day^{-1}$.

Table IV. Mean overall apparent digestibility coefficient ± SD with product type; $n = 30$.

Digestibility parameter	**Mean apparent digestibility coefficient**	
	Wet	**Dry**
Organic matter	0.855 ± 0.025[a]	0.872 ± 0.025[a]
Dry matter	0.821 ± 0.027[a]	0.846 ± 0.024[a]
Protein	0.830 ± 0.027[a]	0.864 ± 0.026[a]
Fat	0.895 ± 0.035	0.902 ± 0.059
Carbohydrate	0.864 ± 0.025	0.872 ± 0.028
Energy	0.853 ± 0.032	0.868 ± 0.027

[a] Product apparent digestibility coefficients which are significantly ($P < 0.05$) different.

into two age-ranges; 9–16 weeks and 19–32 weeks (Tab. II). Between 19 and 32 weeks of age, the kittens were significantly ($P < 0.05$) better at digesting these components than between 9 and 16-weeks.

Newman-Keuls groups for dry-matter, protein and fat encompassed a greater overlap of age-range. Protein fell into two groups resembling those for carbohydrate, organic-matter and energy. However, these groups were not separate, with the mean apparent digestibility coefficient for protein at weeks 14–16 falling into both groups. Apparent digestibility coefficient groups for fat and dry-matter were increasingly diffuse. In the case of dry-matter, the mean apparent digestibility coefficient at age-range 19–21 weeks was significantly higher ($P < 0.05$) than that at 9–11 weeks, with each falling into two separate groups; with both groups including the other three age-ranges. Fat is the only case where mean digestibility coefficients increased in line with age to 24 weeks (Tab. II), although again the two Newman-Keuls groups show overlap.

Relationships between differing energy intakes on apparent digestibility measurements were very weak; correlation coefficients and R squared values determined by simple linear regression analysis ranged from 0.29 to 0.45 and 8 to 20 respectively. Digestible energy showed the strongest of the relationships with a correlation coefficient and R squared value of 0.45 and 20, whilst dry-matter showed the weakest relationship with a correlation coefficient and R squared value of 0.29 and 8 respectively.

Table V. Comparison between species of some digestive processes.

Observation	Species	Comment	Reference
General	Calf	Changes occur in the digestive process at weaning.	16
	Cat	Majority of changes within the gastric mucosa occur during the neonatal period.	In [34]
	Rat	Solid food nibbling plays a role in pancreatic enzyme development: rats denied solid food and whose weaning is postponed have reduced amylase and increased chymotrypsin and lipase concentrations compared to normally weaned rats.	5, 6
Fat	Cat	Low digestibility of fat at weaning.	25
	Cat	Amount and origin of fat determines apparent digestibility	8, 12
	Pig	Lipolytic enzyme expression displays a non parallel pattern of development in the pig: at weaning levels of lipase, colipase and carboxyl ester hydrolase decrease, levels of gastric lipase increase.	10
Carbohydrate	Cat	Cats show a two fold increase in amylase activity following several months adaptation to a starch diet.	18
	Cat	Pancreatic amylase reaches adult levels at 9–12 weeks of age and can be promoted by feeding cooked starch at weaning.	In [8]
	Cat	Cats have all essential enzymes for carbohydrate digestion. There is no clear induction effect in adult cats.	In [8], 21, 22
	Cat	Cats show a two fold increase in amylase activity which takes several months after initiation of a starch diet.	18
	Dog	Dogs show a six fold increase in amylase activity following a 2 week adaptation to a starch diet.	18
	Human	Rate and capacity for absorption of carbohydrate monomers by the small intestine are less efficient in the infant.	14, 33
	Human and Rat	Rate changes in absorption are attributed to change in relative abundance of different transporters, reduced transporter density and changes in transporter activities.	14, 19, 23, 24, 27, 28
Protein	Cat	Increase in the ratio of amino acid to sugar uptake occurs in kittens up to 60 days old.	2
	Cat	Chymotrypsin activity depends on type and amount of proteins fed, and is three times higher than in the dog.	In [8], 9
	Dog	Dogs have a lower capacity for protein digestion than do cats.	18
	Pig	Development on pancreatic proteases after weaning depends on dietary protein source: skim milk powder versus soybean protein concentrate.	17

4. DISCUSSION

4.1. Growth and energy intakes

The present study was primarily performed in order to evaluate the effect of age on apparent digestibility in weaned growing kittens fed two diets. Both diets were equally capable of maintaining kitten growth and there was no significant difference between the growth of the two groups of kittens. Kitten growth was beginning to slow down by the end of the trial period, with a mean change in BW of 230.67 ± 78.67 g at age-range 24–26 weeks opposed to 17.58 ± 70.11 g at 30–32 weeks. Published growth curves suggest kittens do not attain adult BW until at least 40 weeks of age, although approximately 75% of final BW is achieved at 24 weeks [15]. Cats older than 40 weeks of age have a consistent maintenance DE intake requirement [1, 26]. Kittens are considered mature by 40 weeks and thereafter have a consistent maintenance DE intake, so a predicted DE intake of the kittens between 39–41 weeks is representative of the maintenance DE intake throughout the remainder of their life stages [1, 26].

Published maintenance DE daily intakes of inactive and active cats are 293 and 334 $kJ \cdot kg^{-1}$ BW respectively [13]. Comparison of predicted values (Tab. III) with those previously published suggests that the logarithmic-X and reciprocal-Y models more accurately describe the DE intake of the kittens between 39 and 41 weeks for these diets.

For either of these models to accurately predict DE using age-categories representing age-ranges beyond 41 weeks, they should continue to forecast DE intakes similar to those calculated between 39 and 41 weeks of age, which, in the case of these kittens, should be around 307 $kJ \cdot kg^{-1} BW \cdot d^{-1}$. Recalculating the daily DE intake using the logarithmic-X and reciprocal-Y models at age-category 10 (age-range 54–56 weeks), predicts DE values of 210 and 234 $kJ \cdot kg^{-1} BW \cdot d^{-1}$ respectively; figures indicating that these models predict adult maintenance DE intakes exclusively at age-category 7 (age-range 39–41 weeks).

The predictive deficiency of the models beyond 41 weeks is probably a result of the data used to generate the models predominantly representing the DE intakes of rapidly growing kittens only. Although of no more benefit, a model generated from data obtained from kittens through all phases of their growth period may be more accurate over a longer age period.

4.2. Diet and digestibility

No literature exists which compares digestibility or digestibility of different diet formats in kittens, consequently it is not known whether the digestibility coefficients obtained in this study are at the top, middle or bottom of the normal range exhibited by kittens. Therefore, it is impossible to make extrapolations from a single representative of each type of diet.

Apparent digestibilities for energy, fat and carbohydrate were not significantly different between the two diet formats. Protein, dry-matter and organic-matter were significantly ($P < 0.05$) more digestible in the dry product than in the wet, however, there is not a large difference in the overall magnitude of the digestibility coefficients; all lying within the range 0.82 to 0.88 (Tab. IV). Protein is a component of both dry and organic-matter, and increased apparent digestibility of these latter two parameters is most probably due to the increased contribution of the protein digestibility. Apparent digestibility of fat and carbohydrate in these kittens were not influenced by diet. Fat has the highest energy value of the three macronutrients, and carbohydrate has a similar energy value to protein. Their equal apparent digestibility in both diets probably accounts for the lack of difference in the apparent digestibility of energy between the two diets.

Little published data regarding apparent digestibility coefficients exist even in adult cats maintained on dry food, but, apparent digestibility coefficients obtained from sand cats (*Felis margarita*) were in the range 0.7 to 0.8 [4], and in domestic adult cats 0.5 to 0.9 [8]. Published figures for adult cats maintained on wet diets show coefficients between 0.5 to 0.95 [4, 8, 13, 25]. Origin of a macronutrient in the diet has been shown to influence apparent digestibility [8, 11]. In adult cats, apparent digestibility of crude protein is reported to be higher when derived from meats and animal derivatives (0.94–0.97) rather than fish meal or legumes such as soy (0.9). Fats derived from animal offal such as heart and lung have larger (0.9–0.96) apparent digestibility coefficients than those for beef tallow or fish meal, whilst digestibility of carbohydrate is greatest from cereal crops rather than potato [8].

Macronutrients in the diets originated from similar sources for both group of kittens. Protein in the dry diet was derived from both animal derivatives and corn gluten meal, that in the wet was almost solely of animal origin (Tab. I). Difference in protein source may account for the significantly ($P < 0.05$) increased protein digestibility of the dry diet; however, digestibility coefficients of cereal derived protein sources in the cat are not available. Halle [8] states that "in commercial food the digestibility of crude protein is subject to greater variations depending on components and preparation [8]". Inherent differences between the individual diets provide a more plausible explanation for the difference in protein digestibility in this study: a phenomenon that has been previously documented for cat foods [4, 8, 13, 25]. However, the variation in apparent digestibility coefficients reported for adult cats maintained on varying diet formats, underlines the fallibility of over interpreting the single values obtained for the two diet formats in this study; especially, in the absence of any other digestibility data in the kitten. It is not known whether the differences in apparent digestibility obtained in this study reflect typical differences in diet format.

4.3. Age and digestibility

The present study was primarily performed in order to evaluate the effect of age on apparent digestibility in weaned growing kittens fed two commercial diets. Although the adult cat has evolved to survive on a diet containing negligible amounts of carbohydrate, the diet of a suckling kitten contains as much carbohydrate as protein [2]. Cats and older kittens thrive on diets containing significant amounts of carbohydrate amongst their energy sources. In this study, both diets contained similar levels ($g \cdot 400\ kcal^{-1}$) of carbohydrate (Tab. I). There was no significant difference in apparent digestibility of carbohydrate between diet (Tab. IV).

Mean apparent digestibility of all macronutrients analysed were lower in kittens younger than 19 weeks of age, suggesting that more immature kittens are less able to digest solid food; an entelechy reflected by Newman-Keuls multiple range tests, which confirmed that kittens less than 19 weeks of age were significantly ($P < 0.05$) less able to digest energy, carbohydrate and organic-matter than those older than 19 weeks. There were no significant ($P > 0.05$) interactions between diet and age and Newman-Keuls multiple range groups for age-range were calculated irrespective of diet. As significant ($P < 0.05$) differences in the overall apparent digestibility of protein, organic-matter and dry-matter exist between diets (Tab. IV), combining the data generates greater variability within the data set. Greater variability creates more stringent conditions for exclusion of a particular age-range from a homogeneous group. Overlapping homogeneous groups for protein and dry-matter may therefore be partially influenced by the differences between diet.

Mean apparent digestibility coefficients for protein, carbohydrate, organic-matter and dry-matter stabilise by 19 weeks and indicate that digestibility within these kittens has matured. Fat stabilises by 24 weeks suggesting that the required lipases within the kitten's digestive system may develop more slowly (Tab. II).

The gastro-intestinal tract undergoes an intensive period of growth in the early postnatal period, predominantly in the first 24 h after birth [30–32]. In some mammals at weaning, a second period of growth occurs, but, the majority of experimental evidence indicates that dietary changes at weaning modulate levels of enzyme activity rather than initiate intestinal changes [12, 16, 20]. In cats, the majority of changes within the gastric mucosa appear during the neonatal period [34]; literature suggesting that the age related changes in apparent digestibility coefficients observed in this study are more probably due to dietary modulation of enzyme expression rather than maturation of the gastro-intestinal tract. Gut enzyme biochemistry data, and pre-weaning or at weaning apparent digestibility coefficients would be required in order to exclude diet as the major driving force behind the improving apparent digestibility coefficients. Relatively little is known about molecular factors governing macronutrient digestibility in the cat. Further, apparent digestibility coefficients are a crude reflection of the processes occurring within the gastro-intestinal tract and do not exclude the impact of colonic fermentation on digestibility. Therefore, only general comments may be made in relation to possible age related factors driving changes in apparent digestibility; with some of the ideas being derived from data generated by other mammalian species (Tab. V).

It is clear that in general absorption of carbohydrate monomers by monosaccharide transporters in the small intestine are related to postnatal age. Generally, rate and capacity for absorption are less efficient in the infant compared to the adult (Tab. V) [14, 19, 23, 24, 27, 28, 33].

In the kitten, during suckling, pancreatic proteolytic activity remains constant whilst amylase activity increases during the first month of life [18] and therefore, during the suckling period at least, kittens express the requisite enzymes and transporters to digest carbohydrates. Age-related increases in the ratio of amino acid to sugar uptake occur in kittens; a reflection of the natural decline of carbohydrate from the diet [2]. However, the carbohydrate content of the diet used to maintain the queens and kittens in this study appears almost negligible [2], and therefore it is impossible to predict whether a similar decrease in sugar transporters would have been observed had the maintenance diet contained more carbohydrate. Certainly, inductive effects of substrates on enzymes associated with carbohydrate digestion do occur in the cat, although small when compared to the dog (Tab. V) [18]. Further, in the rat, solid food nibbling has been reported to play a role in pancreatic enzyme development (Tab. V) [5, 6].

In the present study kittens had access to their mother's food prior to weaning, and although significantly less able to digest carbohydrate, and consequently organic-matter and energy between 9 and 19 weeks (Tab. IV), mean apparent digestibility coefficients of carbohydrate stabilised at a younger kitten age, than previously reported [21, 25]. It is possible to hypothesise that such access to food may have stimulated both pancreatic enzyme development, and, increases in the requisite sugar transporters, consequently resulting in better carbohydrate digestibility after weaning than seen in kittens denied or with less access to solid food [5, 6, 18]. Requirement for both pancreatic amylase and development of the requisite monosaccharide transporters may be the reason why in previous studies carbohydrate digestibility took longer to stabilise [21, 25].

Fat is the only macronutrient whose mean apparent digestibility increases with age up to 24 weeks. The gradual rise of mean apparent digestibility of fat with age compares well with data from other studies [21, 25].

Bile-salt activated lipase is a component of cat milk, and evidence suggests that this plays a role in the fat digestion process of the new-born [29]. Its presence in cats' milk further suggests that pancreatic lipase levels are low in the new-born. There are no reports of pancreatic lipase development in the cat, but the presence of bile-salt activated lipase in cat milk and reports of low fat digestibility in the kitten at weaning indicate that lipase development may be slow in the cat. Alternatively, the cat may display a similar type of lipolytic enzyme development to the pig: a non parallel pattern, suggested to reflect the importance of the different enzymes at the suckling and post-weaning phases (Tab. V) [10, 25, 29].

In conclusion, although factors such as increased length and surface area of the intestine and transit time of macronutrients through the gut will influence apparent digestibility of the diet during the growth period of the kittens, the developmental patterns of the lipolytic enzymes and carbohydrate monosaccharide transporters reported over the weaning period in other mammals may be applicable to the kitten (Tab. V). Further, delay in maturation of fat digestibility compared to the other macronutrients, and, differences in the patterns of the homogeneous groupings obtained by Newman-Keuls multiple range tests indicates that apparent digestibility is influenced by factors additional to increased transit time and surface area of the intestine. If only physical factors were involved then apparent digestibility of each macronutrient could be expected to mature simultaneously, and the pattern of maturation should be comparable.

The newly weaned kitten faces the challenge of dietary induced enzyme modulation along with final maturation of the lipolytic enzymes and carbohydrate transporters, and it is not surprising that the apparent digestibility of macronutrients is low. Also, carbohydrate would not normally contribute a large part of the cat's natural diet and therefore maturation of the carbohydrate digestive system in the kitten may be slower than in species who rely upon carbohydrates as their main energy source. The majority of macronutrients reach adult apparent digestibility coefficients at 19 weeks with fat at 24 weeks, the latter presumably due to the length of time required to both switch and then modulate the level of the required lipolytic enzyme.

These observations are important for kitten growth. It is obviously important to ensure that kittens are provided with good quality digestible foods to compensate for their relatively immature digestive systems. There was no significant ($P > 0.05$) difference between the growth rates supported by the two diets despite differences in their carbohydrate and fat content. Therefore diets with fat and carbohydrate contents with these ranges support kitten growth and development. This study shows kittens are capable of coping with diets containing carbohydrate. However other work has indicated that adaptation to a carbohydrate containing diet may be slow [2, 18]. Gastrointestinal problems are frequently associated with poorly digestible diets. Increasing the fat and carbohydrate content of a kitten diet beyond the digestive capacity of the kitten small intestine, or swapping between diets of very different macronutrient profiles could lead to gastrointestinal disturbance. It is therefore recommended that new food formats are introduced gradually into the kitten's diet, particularly for those aged less than 19 weeks.

ACKNOWLEDGEMENTS

The authors thank Professor G. Gettinby for help with statistical analysis, and R. Butterwick, V. Rolfe, C. Giffard, G. Perez and J. Hare for helpful discussions and critical comments with this manuscript. We also wish to thank all the animal carers for kitten care and V. Legrand-Defretin for the French translation.

REFERENCES

[1] Anantharaman-Barr H.G., Gicquello P., Rabot R., The effect of age on the digestibility of macronutrients and energy in cats, Proc. Br. Small Anim. Vet. Assoc. Congress, 1991, p. 164.

[2] Buddington R.K., Diamond J., Ontogenetic development of nutrient transporters in cat intestine, Am. J. Physiol. 263 (1992) G605–616.

[3] Burger I., The Waltham Book of Companion Animal Nutrition, Pergamon Press, Oxford, UK, 1993, ISBN 0-08-040803-5.

[4] Crissey S.D., Swanson J.A., Lintzenich B.A., Brewe B.A., Slifka K.A., Use of a raw meat-based diet or a dry kibble diet for Sand Cats (*Felis margarita*), J. Anim. Sci. 75 (1997) 2154–2160.

[5] Dumont Y., Larose L., Poirier G.G., Morisset J., Effect of early weaning of the neonatal rat on pancreatic acinar cell responsiveness to urecholine, Digestion 17 (1978) 323–331.

[6] Dumont Y., Larose L., Poirier G.G., Morisset J., Delayed weaning and denial of solid food nibbling upon pancreatic acinar cell responsiveness to urecholine in neonatal rats, Digestion 18 (1978) 93–102.

[7] Gilham M.S., Booles D., Johnson J.V., Legrand-Defretin V., Digestibility in Labrador Retrievers during growth, Proc. Nutr. Soc. 52 (1993) 294 (abs.).

[8] Halle I., Nutrition of the cat, J. Vet. Nutr. 1 (1992) 17–30.

[9] Hicks C.R., Fundamental Concepts in the Design of Experiments, 4th ed., Oxford University Press, Inc., New York, 1993, ISBN 0-19-510581-8.

[10] Jenson M.S., Jenson S.K., Jakobsen K., Development of digestive enzymes in pigs with emphasis on lipolytic activity in the stomach and pancreas, J. Anim. Sci. 75 (1997) 437–445.

[11] Kane E., Morris J.G., Rogers Q.R., Acceptability and digestibility by adult cats of diets made with various sources and levels of fat, J. Anim. Sci. 53 (1981) 1516–1523.

[12] Kelly D., Smyth J.A., McCracken K.J., Digestive development in the early weaned pig, Br. J. Nutr. 65 (1991) 169–180.

[13] Kendall P.T., Blaza S.E., Smith P.M., Comparative Digestible Energy Requirements of Adult beagles and Domestic Cats for Body Weight Maintenance, J. Nutr. 113 (1983) 1946–1955.

[14] Kojima T., Nishimura M., Yajima T., Kuwata T., Suzuki Y., Goda T., Tahase S., Harada E., Developmental changes in the regional Na^+/glucose transporter mRNA along the small intestine of suckling rats. Comp. Biochem. Physiol. B Biochem. Mol. Biol. 122 (1999) 89–95.

[15] Legrand-Defretin V., Munday H.S., Feeding dogs and cats for life, in: Burger I. (Ed), The Waltham Book of Companion Animal Nutrition, Pergamon Press, Oxford, UK, 1993, p. 64, ISBN 0-08-040803-5.

[16] Le Huërou-Luron I., Guilloteau P., Wicker-Planquart C., Chayvialle J.-A., Burton J., Mouats A., Toullec R., Puigserver A., Gastric and pancreatic enzyme activities and their relationship with some gut regulatory peptides during postnatal development and weaning in calves, J. Nutr. 122 (1992) 1434–1445.

[17] Makkink C.I., Berntsen P.J., Op den Kamp B.M., Kemp B., Verstegen M.W., Gastric protein breakdown and pancreatic enzyme activities in response to two different dietary protein sources in newly weaned pigs, J. Anim. Sci. 72 (1994) 2843–2850.

[18] Meyer H., Kienzle E., Dietary protein and carbohydrates: Relationship to clinical disease, Purina International Nutrition Symposia, January 15, 1991, Orlando, Florida.

[19] Milla P.J., Atherton D.A., Leonard J.V., Wolff O.H, Lake B.D, Disordered intestinal function in glycogen storage disease, J. Inherited Metab. Dis. 1 (1978) 155–157.

[20] Morisset J., Regulation of growth and development of the gastrointestinal tract: regulation of function and metabolism, J. Dairy. Sci. 76 (1993) 2080–2093.

[21] Munday H.S., Lowe B.K., The digestibility of macronutrients in the growing domestic cat, Proc. Nutr. Soc. 52 (1993) 275 (abs.).

[22] Nutrient Requirements of Cats, Rev. Ed. National Academy Press, Washington D.C., 1986, ISBN 0-309-03682-8.

[23] Puchal A.A., Buddington R.K, Postnatal development of monosaccharide transport in pig intestine, Am. J. Physiol. 262 (1992) G895–G902.

[24] Rey F., Drillet J., Schmitz J., Rey J., Influence of flow rate on the kinetics of intestinal absorption of glucose and lysine in children, Gastroenterology 66 (1974) 79–85.

[25] Skinner N.D., Taylor E.J., Digestive efficiency of kittens and juvenile cats, Proc. FENS Meeting, Vienna, Austria, May 1995.

[26] Taylor E.J., Adams C., Neville R., Some nutritional aspects of ageing in cats and dogs, Proc. Nutr. Soc. 54 (1995) 645–656.

[27] Thomson A.B., Keelan M., The development of the small intestine, Can. J. Physiol. Pharmacol. 64 (1986) 13–29.

[28] Toloza E.M., Diamond J., Ontogenetic development of nutrient transporters in rat intestine, Am. J. Physiol. 263 (1992) G593–G604.

[29] Wang C.S., Martindale M.E., King M.M., Tang J., Bile salt activated lipase: effect on kitten growth rate, Am. J. Clin. Nutr. 49 (1989) 457–463.

[30] Xu R.J., Development of the new-born GI tract and its relation to colostrum milk intake: A review, Reprod. Fertil. Dev. 8 (1996) 35–48.

[31] Xu R.J., Mellor D.J., Tungthanathanich P., Birtles M.J., Reynolds G.W., Simpson H.V., Growth and morphological changes in the small and large intestine in piglets during the first three days after birth, J. Dev. Physiol. 18 (1992) 161–172.

[32] Xu R.J., Tungthanathanich P., Birtles M.J., Mello, D.J., Reynolds G.W, Simpson H.V., Growth and morphological changes in the stomach of the new-born pigs during the first three days after birth, J. Dev. Physiol. 17 (1992) 7–14.

[33] Younoszai M.K., Jejunal absorption of hexose in infants and adults, J. Pediatr. 85 (1974) 446–448.

[34] Zabielski R., Le Huërou-Luron I., Guilloteau P., Development of gastrointestinal and pancreatic functions in mammalians (mainly bovine and porcine species): influence of age and ingested food, Reprod. Nutr. Dev. 39 (1999) 5–26.