Carbohydrate digestion by the domestic cat (*Felis catus*)

By J. G. MORRIS, JEANETTE TRUDELL AND TERRI PENCOVIC

*Departments of Animal Science and Physiological Sciences,
University of California, Davis, California 95616, USA*

1. Three experiments were conducted on the ability of cats to utilize dietary carbohydrates. In two experiments, the digestibilities of carbohydrates were measured by the chromic oxide-marker technique using a balanced Latin-Square allocation of treatments: in the third experiment, the effect of age and diet on the activity of intestinal β-galactosidase (lactase) (*EC* 3.2.1.23) and β-fructofuranosidase (sucrase) (*EC* 3.2.1.26) of kittens was measured.

2. In Expt 1 the digestibilities of six individual carbohydrates, glucose, sucrose, lactose, dextrin, raw maize starch and wood cellulose added to a meat-based basal diet were measured.

3. In Expt 2, a similar meat-based basal diet was used and the effect of three processing methods (fine and coarse grinding, and cooking) on the apparent digestibility of the starch in maize and wheat grain was measured.

4. In Expt 3 the effects of the inclusion of either 200 g lactose or 200 g sucrose/kg in an all-meat diet and of age on the β-galactosidase and β-fructofuranosidase activities of the small intestine of weanling kittens were measured.

5. Adult cats efficiently (> 0·94) digested all six individual carbohydrates added to the diet with the exception of cellulose, which was indigestible. The digestibility coefficients of glucose, sucrose and lactose were significantly ($P < 0·01$) greater than that of starch. The inclusion of lactose caused diarrhoea in some cats and significantly ($P < 0·01$) reduced apparent digestibility of crude protein (nitrogen × 6·25) in the total ration.

6. Fine grinding significantly enhanced the digestion of starch in wheat and maize grain, but the effect was greatest for maize grain. Cooking had a similar effect to fine grinding for wheat grain, but an effect intermediate between coarse and fine grinding for maize grain.

7. Intestinal β-galactosidase activity decreased with age in kittens (71-106 d). Neither β-fructofuranosidase nor β-galactosidase activities were significantly affected by the addition of sucrose and lactose to the all-meat diet.

Even though extensive use has been made of the cat in physiological research, and the large pet-food industries in the UK and North America, there is little quantitative information on the nutrient requirements of the cat or other Felidae, nor on their ability to utilize major classes of feedstuffs. A number of investigators have reported the use of rations containing carbohydrate-rich foods or individual carbohydrates, e.g. potatoes (DaSilva, 1950; Dawson, 1950; Dickinson & Scott, 1956), sucrose (Allison, Miller, McCoy & Brush, 1956; Gershoff, Andrus & Hegsted, 1959), glucose (Allison *et al.* 1956; Miller & Allison, 1958) and dextrin (Miller & Allison, 1958; Greaves & Scott, 1963), but there have been no measurements reported on the extent to which carbohydrates are digested and utilized by the cat. Commercial cat diets, especially of the dry type, may contain similar amounts of starch and protein. Eight commercial dry diets which we analysed were found to contain (g/kg dry diet; mean ± SE) 342 ± 18 starch (glucose measured by the *o*-toluidine method after perchloric acid hydrolysis) and 344 ± 3 crude protein. A semi-moist diet and a canned diet were found to contain 360 and 126 g starch/kg dry weight, respectively.

This paper reports the utilization by the cat of six individual carbohydrates, glucose,

Table 1. *Chemical composition (g/kg dry matter) (by analysis) of the diets containing individual carbohydrates used in Expt 1*

Diet	Crude protein (nitrogen × 6·25)	Light petroleum extract	Ash	Glucose*	Saccharide (di- or poly-)
Basal	449	442	83	12	6
Glucose	366	334	63	234	5
Sucrose	337	323	65	14	229
Lactose	334	326	60	41	229
Dextrin	344	333	62	15	198
Starch	346	338	61	11	222
Cellulose	338	333	57	10	227

* *o*-toluidine-reactive glucose; for details, see p. 368.

sucrose, lactose, dextrin, maize starch and cellulose, and of the starch in wheat and maize grain as affected by fineness of grinding and by cooking. The effect of age and the inclusion of sucrose and lactose in the postweaning diet of kittens on the β-fructofuranosidase (*EC* 3.2.1.26) and β-galactosidase (*EC* 3.2.1.23) activities of the small intestine were also measured.

MATERIALS AND METHODS

Diets

All diets were prepared in bulk before the commencement of each experiment and frozen in plastic bags.

Expt 1. A basal diet was prepared from fresh minced meat (a mixture of beef and mutton) to which was added (/kg) 5 g calcium carbonate, 2·5 g chromic oxide and 12·5 μg cholecalciferol. The experimental diets were prepared by mixing the carbohydrate with the basal diet (1:7 w/w). The compositions of the diets are shown in Table 1.

The individual commercial carbohydrates used were: glucose (Cerelose 2001; CPC International Inc., Industrial Division, Englewood Cliffs, New Jersey 07632, USA), sucrose (California & Hawaii Sugar Company, San Francisco, California 94106, USA), lactose (Formost Foods Co., Appleton, Wisconsin, USA), dextrin (Nutritional Biochemical Corp., Cleveland, Ohio, USA), starch (raw maize starch) (Pearl Starch; A. E. Staley Mfg. Co., Decatur, Illinois, USA), cellulose (wood cellulose) (Solka-Floc; Brown & Co., Berlin, New Hampshire, USA).

Expt 2. A basal diet was prepared from minced horse meat to which was added (g/kg) 100 ground green bone (to increase the consistency of the faeces and to supply calcium), 2·5 chromic oxide, 3·3 complete vitamin mixture ((US) National Research Council, 1972). The experimental diets were prepared by adding 150 g air-dry grain to each 1 kg basal diet.

The wheat and maize were ground through a hammer mill and sieved; the fraction which passed through a sieve with 2 mm opening and was retained by a sieve with 0·84 mm openings was retained. This was designated as coarsely-ground grain. About one-third of this fraction was then milled in a Wiley mill fitted with a 1 mm screen

Table 2. *Chemical composition (g/kg of dry matter) (by analysis) of the maize and wheat grain and of the basal diet used in Expt 2*

	Organic matter	Crude protein (nitrogen × 6·25)	Light petroleum extract	Starch	Free glucose
Maize	987	104	42	794	2·4
Wheat	983	150	15	792	1·2
Basal diet	902	517	368	2·9	ND

ND, not determined.

and the product constituted the finely-ground grain. Another one-third of the coarsely-ground grain was moistened with water then autoclaved at 100 kN/m² for 45 min. This was designated as cooked grain. The composition of the two grains is given in Table 2.

Expt 3. Three diets were prepared from a large quantity of fresh, minced beef to which 10 g calcium carbonate/kg had been added. Two diets were prepared by mixing either 200 g sucrose (California & Hawaii Sugar Company) or 200 g lactose (Foremost Foods) with each 800 g beef, whereas the third diet had no added carbohydrate. To all three diets a vitamin premix was added in amounts to supply the (US) National Research Council (1972) recommended requirements on a dry matter basis.

Animals

Expt 1. Six nearly mature, domestic, short-haired cats (five males and one female), mean body-weight 3·4 kg, were used. They had all been inoculated with panleucopenia vaccine (Felocell; Norden Laboratories, Lincoln, Nebraska, USA) and treated with piperazine adipate as an anthelmintic. All cats were in good health throughout the experiment, except for the diarrhoea induced by the lactose diet.

Expt 2. Eight nearly mature, domestic, short-haired cats (four males and four females), mean body-weight about 3 kg, were used. Six of the cats were housed in separate cages, two females were housed together in one cage and two males in another cage. All cats had received the same inoculation and anthelmintic treatment as described for Expt 1.

Expt 3. Fourteen short-haired kittens weaned at 8 weeks of age were prepared by giving the same inoculations and anthelmintic treatment as used in Expt 1.

Housing and faecal collection

In Expts 1 and 2 steel cages (1·4 × 0·6 × 0·8 m) were used to house the animals. In Expt 1 the litter-boxes were plastic dish-pans (0·35 × 0·30 × 0·17 m) containing vermiculite, and the faeces were recovered daily by sifting the litter through a wire screen. In Expt 2 the same plastic dish-pans containing washed, shredded cotton cloth were used as litter-boxes, and the faeces were removed daily. Freshly washed cotton cloth was added daily and the soiled cotton cloth removed. In both experiments faeces were stored at −10° until the end of the experiment, when they were lyophilized and prepared for analysis.

The cats in Expt 3 were housed in stainless-steel cages ($0.6 \times 0.6 \times 0.9$ m) with wood shavings as litter. They were weighed at weekly intervals and on the day on which they were killed to obtain the intestine.

Analytical methods

For the measurement of apparent digestibility, food and faecal samples were lyophilized and then extracted with light petroleum (b.p. 30–60°) for 2 weeks in a macro-soxhlet apparatus. After milling 1 g of each sample was extracted three times with 50 ml hot ethanol–water (80:20, v/v) to remove soluble sugars. Free reducing sugars were determined in an alcohol-free portion of this extract, using the ferricyanide procedure of Hoffman (1937) modified for automated analysis (Technicon Instrument Corp., 1967). By the same method, total reducing sugars were determined after hydrochloric acid-hydrolysis of a portion of the extract. For the disaccharide-containing diets, the appropriate factors were used to convert the glucose equivalent to sucrose and lactose.

The residues after ethanolic extraction were suspended in water, heated in a boiling water-bath, cooled and then extracted three times with 25 ml 4.4 M-perchloric acid to remove starch or dextrin. Reducing sugars were measured on the extract before and after acid-hydrolysis and the difference was attributed to starch or dextrin. The o-toluidine procedure (Yee & Jenest, 1969) was also used to determine glucose using the AutoAnalyzer (Technicon Instrument Corp., Tarry Town, New York, USA), and showed good agreement with the ferricyanide method. Nitrogen and ash were measured by the methods of the Association of Official Agricultural Chemists (1960).

In Expt 1, faecal and food samples were digested in a nitric acid–perchloric acid mixture and analysed for chromium by colorimetry. Residual vermiculite contamination gave abberant results when atomic absorption spectrophotometry was used. In Expt 2, atomic absorption spectrophotometry (Arthur, 1970) was used to measure the Cr, since vermiculite was not used as litter. Apparent digestibilities of the carbohydrates were measured by the ratio, Cr_2O_3:carbohydrate in food and faeces:

$$\text{Apparent digestibility} = 1 - \frac{Cr_2O_3 \text{ in food (g/kg)} \times \text{carbohydrate in faeces (g/kg)}}{Cr_2O_3 \text{ in faeces (g/kg)} \times \text{carbohydrate in food (g/kg)}}.$$

Kittens were anaesthetized by an intra-abdominal injection of pentobarbital sodium and when the pedal reflex was absent a laparotomy was performed and the intestine rapidly removed and placed on crushed ice. The intestine was then opened longitudinally and washed with chilled 0.15 M-saline (sodium chloride) to remove the contents. After removal of excessive moisture by blotting with paper towels, the mucosa was removed by scraping.

The β-galactosidase and β-fructofuranosidase activities of the small intestine were measured by the method of Dahlqvist (1964) as modified by Manners & Stevens (1972). The glucose released on hydrolysis of the lactose and sucrose was measured by the glucose oxidase method (Glucostat; Worthington Biochemical Corporation, Freehold, New Jersey 07728, USA). The protein content of the intestinal mucosal homogenates was measured by the biuret method of Weichselbaum (1946) modified

for the AutoAnalyzer (Technicon Instrument Corp., 1969). The small intestine (from the pylorus to the ileo-caecal junction) was divided into four sections of equal length. The mucosa from the upper first and second segments of intestine was removed for the assay of enzyme activity.

Design

In both Expt 1 and Expt 2 each cat received all six carbohydrate-containing diets in a balanced Latin-Square sequence (Cochran & Cox, 1957). In Expt 1, a 3 d preliminary period preceded the 7 d collection period whereas in Expt 2, 5 d preliminary and 5 d collection periods were used. In both experiments the basal ration was given for 10 d before the first carbohydrate-containing diet and 10 d after the last carbohydrate-containing diet.

Results were analysed as a balanced Latin Square, and 'carry-over' effects were estimated. Tables 3 and 4 give the least significant differences, calculated by the method of Steel & Torrie (1960).

In Expt 3, kittens were allocated on the basis of age, litters and sex until there were five kittens receiving each of the carbohydrate diets and four kittens receiving the control diet. Kittens from all three treatments were killed at the following ages: 71, 96, 94 and 106 d, and also for those from the groups given lactose- and glucose-containing diets at 109 d.

Linear regression coefficients of the enzyme activity expressed on a per mg protein per min. basis, *v.* age (d) were computed.

RESULTS

Individual carbohydrates. All cats readily accepted the rations and maintained a daily food intake of about 170 g moist ration. The apparent digestibility coefficients of organic matter, crude protein (N × 6·25), light petroleum extract and carbohydrates are given in Table 3. Dietary 'carry-over' effects were not significant ($P < 0.05$) for any of the measurements. All the carbohydrates with the exception of cellulose had high digestibility coefficients, but starch was digested significantly ($P < 0.01$) less efficiently than glucose, sucrose, lactose or dextrin. The apparent digestion coefficient for starch 0·942, (Table 3) was the mean value for all six cats. However, one cat had a very low digestion coefficient (0·845), eliminating this, the mean value for the other five cats was 0·958.

The light petroleum extract component of the complete diets had a uniformly high digestibility coefficient and while there were significant differences between diets containing the various carbohydrates, these differences were small. The apparent digestibility coefficient of crude protein in the lactose-containing diet (0·881) was significantly ($P < 0.01$) less than that in the diets containing the other carbohydrates. The digestibility of the crude protein of the starch-containing diet was significantly less than that in the glucose-, sucrose- and dextrin-containing diets. Cats given the lactose-containing diet had very moist faeces and at times diarrhoea. In a preliminary experiment in which higher levels of lactose were included in the diet than in this experiment, all cats had diarrhoea.

Table 3. *Expt 1. Apparent digestion coefficients of the added individual carbohydrates and of other components of the diet for cats*

(Mean values for six cats/dietary treatment)

Dietary treatment None (basal) ($\pm$ SEM)	Organic matter 0·883 ± 0·0067	Crude protein (nitrogen × 6·25) 0·944 ± 0·0021	Light petroleum extract 0·993 ± 0·0001	Carbohydrate
Glucose	0·923	0·939	0·990	0·998
Sucrose	0·913	0·923	0·989	0·998
Lactose	0·868	0·881	0·990	0·991
Dextrin	0·914	0·923	0·989	0·976
Starch	0·884	0·909	0·990	0·942
Cellulose	0·504	0·926	0·994	−0·007
SEM	0·0067	0·0038	0·0002	0·0088
Least significant difference for carbohydrate-containing diets:				
$P < 0.05$	0·0197	0·0111	0·0007	0·0258
$P < 0.01$	0·0268	0·0151	0·0009	0·0352

Table 4. *Expt 2. Apparent digestion coefficients of added maize and wheat starch and of other components of the diet for cats*

(Mean values for six cats/dietary treatment)

Starch source	Treatment* Grinding		Starch	Crude protein (nitrogen × 6·25)	Organic matter†	Dry matter†
Maize	Coarse	Raw	0·794	0·869	0·746	0·681
	Fine	Raw	0·937	0·880	0·815	0·745
	Coarse	Cooked	0·881	0·871	0·785	0·718
Wheat	Coarse	Raw	0·925	0·887	0·816	0·752
	Fine	Raw	0·972	0·895	0·834	0·777
	Coarse	Cooked	0·962	0·900	0·842	0·771
SEM			0·0148	0·0037	0·0063	0·0047
Least significant difference:						
$P < 0.05$			0·0436	0·0110	0·0185	0·0138
$P < 0.01$			0·0596	0·0150	0·0253	0·0188

* For details, see p. 366.
† Organic matter and dry matter are on a light petroleum extract-free basis.

Maize and wheat starch. The apparent digestibility coefficients of the maize and wheat starch and other components of the diet as affected by grinding and by cooking are given in Table 4. None of the possible 'carry-over' effects of the previous diet on digestibility of the subsequent diet were significant.

The starch from finely-ground maize had a significantly ($P < 0.01$) higher digestibility coefficient than from coarsely-ground grain. The same effect was present with wheat grain and was significant ($P < 0.05$). Fine grinding and cooking significantly

increased digestion of crude protein of maize and with wheat, cooking also had a significant effect. Grinding and cooking also increased the digestibility of light petroleum extract-free organic matter and dry matter.

β-galactosidase and β-fructofuranosidase activities. The β-galactosidase activities of both the first and second segments of the intestinal mucosa decreased with age in all kittens, irrespective of whether the diet contained lactose, sucrose or no added carbohydrate. The linear regression of activity in the first segment of the intestine of all kittens in relation to age (71–109 d) was: $y = 111·6 - 34·7x$, where y is enzyme activity (μM glucose released/min per mg protein) and x is age (d). The correlation coefficients of enzyme activity $v.$ age for first and second segments were both significant ($P < 0·01$), r $-0·74$ and $-0·73$, respectively.

The regression coefficients of β-fructofuranosidase activity $v.$ age were small and negative, but the correlation coefficient was not significant for either segment ($P < 0·05$). The intercepts for the regression of enzyme activity $v.$ age for β-galactosidase and β-fructofuranosidase were similar.

DISCUSSION

The measurements of the digestibility of individual carbohydrates indicate that despite the low carbohydrate content of carnivorous diets characteristic of the Felidae (Ewer, 1973), the cat efficiently digests glucose, sucrose, lactose, dextrin and starch. The apparent digestibility coefficients of these individual carbohydrates is comparable to the digestibility of the gross energy of high-carbohydrate foods by swine, e.g. wheat flour 0·92–0·94, sugar-cane molasses 0·93 ((US) National Research Council, 1968), and the reported apparent digestibility of starch (0·95) by the dog (Rieder, 1884 quoted by McCay, 1949).

The inability of the cat to digest cellulose could be expected because of the relatively short length of the gastrointestinal tract, and presumably short transit time. Some digestion of cellulose (Solka-Floc) occurs in pigs; Cunningham, Friend & Nicholson (1962) reported a digestibility value of 0·18 for maintenance and a value of 0·05 during the late growing period. The essentially zero digestibility which we recorded for cellulose indicates that the Cr_2O_3 technique does not over-estimate digestibility in the cat.

The significant reduction in apparent digestibility of crude protein of the whole diet by the inclusion of lactose is interpreted as a consequence of unassimilated lactose reaching the large intestine and enhancing microbial growth. This hypothesis is supported by the enhanced hydrogen gas production found in β-galactosidase-deficient humans given a test dose of lactose (Calloway, Murphy & Bauer, 1969). As degradation products of lactose, e.g. lactic acid, were not measured, there can be no differentiation between assimilation and fermentation of the lactose. The dog also is unable to tolerate high levels of lactose. Both McCay (1949) and Bennett & Coon (1966) reported that high levels of lactose in the diet of dogs produced diarrhoea. The significant 'between-animal' differences in the apparent digestion coefficients for crude protein arise primarily from differences occurring from the lactose-containing diet. This is

interpreted as an effect of individual differences in lactose digestion and presumably β-galactosidase activity of the small intestine of the six cats.

Our results showing a decrease in β-galactosidase activity of the intestinal mucosa with age of the postweaned kittens are in agreement with those reported by Hore & Messer (1968). They studied the activity in cats ranging in age from newborn to adult and concluded that a sharp decrease in β-galactosidase activity occurs at approximately 4–7 weeks. It would appear from both the results of Hore & Messer (1968) and our results that considerable 'between-animal' variation occurs in the lactase activity of the intestinal mucosa, which would account for the observed individual variation in susceptibility to diarrhoea from lactose-containing diets.

The inclusion of lactose in the diet had no significant effect on the rate of decrease in β-galactosidase activity of the intestine of kittens with age. These results are consistent with those reported in man (Rosensweig & Herman, 1968) but do not agree with those reported by Sriratanaban & Thayer (1970) that postweanling rats given a diet containing 80 g lactose/kg had higher jejunal β-galactosidase than those given a control diet.

An enhancement of digestion of native starch in grains resulting from crushing or grinding the whole grain has been reported or recommended for a number of farm animals (Morris, 1966; McDonald, Edwards & Greenhalgh, 1973). However, the effect of fineness of the grind on digestion is less clear. Our results with cats indicate that for uncooked maize grain, the digestibility of the starch is significantly reduced if the grain is not finely ground. The increase found in digestion is apparently due to physical exposure of the starch to enzymic action, for fine grinding of maize gave a greater enhancement of digestibility over coarse grinding than cooking.

REFERENCES

Allison, J. B., Miller, S. A., McCoy, J. R. & Brush, M. K. (1956). *N. Am. Vet.* **37**, 38.
Arthur, D. (1970). *Can. Spectrosc.* **15**, 134.
Association of Official Agricultural Chemists (1960). *Official Methods of Analysis*, 9th ed. Washington, D.C.: Association of Official Agricultural Chemists.
Bennett, M. J. & Coon, E. (1966). *J. Nutr.* **88**, 163.
Calloway, D. H., Murphy, E. L. & Bauer, D. (1969). *Am. J. dig. Dis.* **14**, 811.
Cochran, W. G. & Cox, G. M. (1957). *Experimental Designs*, 2nd ed., p. 133. New York: John Wiley & Sons Inc.
Cunningham, H. M., Friend, D. W. & Nicholson, J. W. G. (1962). *Can. J. Anim. Sci.* **42**, 167.
Dahlqvist, A. (1964). *Analyt. Biochem.* **7**, 18.
DaSilva, A. C. (1950). *Acta Physiol. latinoam.* **1**, 20.
Dawson, A. B. (1950). In *The Care and Breeding of Laboratory Animals*, p. 206 [E. J. Farris, editor]. New York: John Wiley & Sons Inc.
Dickinson, C. D. & Scott, P. P. (1956). *Br. J. Nutr.* **10**, 304.
Ewer, R. F. (1973). *The Carnivores*, p. 205. Ithaca, New York: Cornell University Press.
Gershoff, S. M., Andrus, S. B. & Hegsted, D. M. (1959). *J. Nutr.* **68**, 75.
Greaves, J. P. & Scott, P. P. (1963). *Proc. Nutr. Soc.* **22**, IV.
Hoffman, W. S. (1937). *J. biol. Chem.* **120**, 51.
Hore, P. & Messer, M. (1968). *Comp. Biochem. Physiol.* **24**, 717.
McCay, C. M. (1949). *Nutrition of the Dog*. New York: Comstock Publ. Co.

McDonald, P., Edwards, R. A. & Greenhalgh, J. F. D. (1973). *Animal Nutrition*, 2nd ed. New York: Hafner Publish. Co.

Manners, M. J. & Stevens, J. A. (1972). *Br. J. Nutr.* **28**, 113.

Miller, S. A. & Allison, J. B. (1958). *J. Nutr.* **64**, 493.

Morris, J. G. (1966). *Qd agric. J.* **92**, 225.

National Research Council (1968). *Publs natn. Res. Coun., Wash.* No. 1599.

National Research Council (1972). *Publs natn. Res. Coun., Wash.* No. 2028.

Rosensweig, N. S. & Herman, R. H. (1968). *J. clin. Invest.* **47**, 2258.

Sriratanaban, A. & Thayer, W. (1970). *Clin. Res.* **18**, 389.

Steel, R. G. D. & Torrie, J. H. (1960). *Principles and Procedures of Statistics*. New York: McGraw-Hill Book Co. Inc.

Technicon Instrument Corp. (1967). *AutoAnalyzer Method* N9a. Tarry Town, New York: Technicon Instrument Corp.

Technicon Instrument Corp. (1969). *AutoAnalyzer Method* N14b. Tarry Town, New York: Technicon Instrument Corp.

Weichselbaum, T. E. (1946). *Am. J. clin. Path.* **7**, 40.

Yee, H. Y. & Jenest, E. S. (1969). *Technicon International Congress. Advances in Automated Analysis*, p. 69. Tarry Town, New York: Technicon Instrument Corp.