The ancestral diet of carnivores

What can we learn for our dogs & cats?

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Content

1. **Introduction**
2. Composition of diets of wild carnivores
3. Translation to domestic dogs & cats
4. Composition of traditional diets
5. Macronutrient effect on health

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Taxonomy & feeding habits

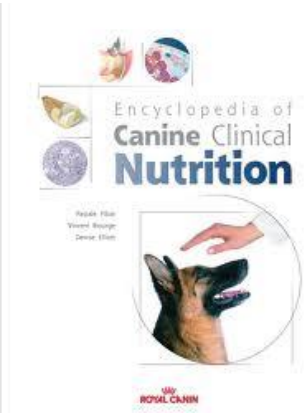
Order Carnivora

- Felidae
  - cheetah, puma, cat, jaguar, lynx, lion, tiger,…
  - **Carnivores**
- Canidae
  - Dog, jackhals, coyote, fox, wolf
  - **Omnivores**
- Ailurpodidae
  - panda’s
  - **Herbivores**



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Dogs <-> cats: strict carnivores



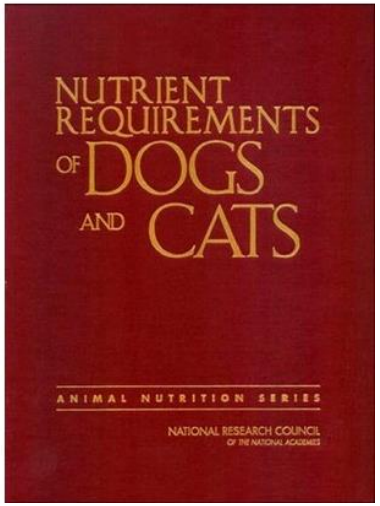
Ancestors => wolves

- Hoof animals as prey
- Eating faeces of herbivores prey
- Eating fruits, berries, mushrooms etc.

Dogs are also opportunistic eaters



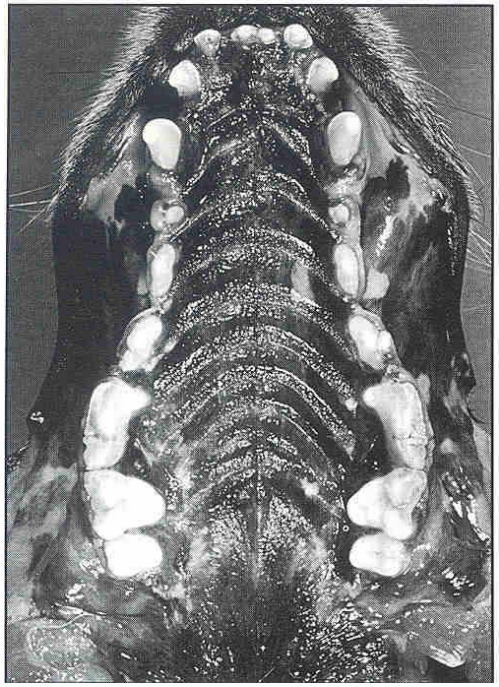
Nutrient req., teeth etc. <-> cats

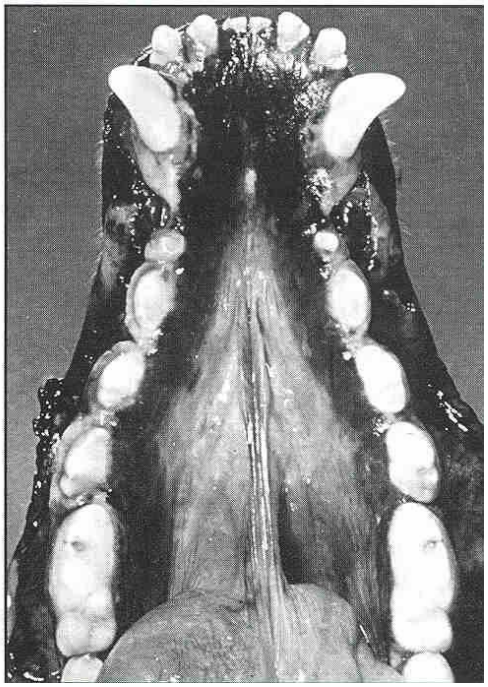


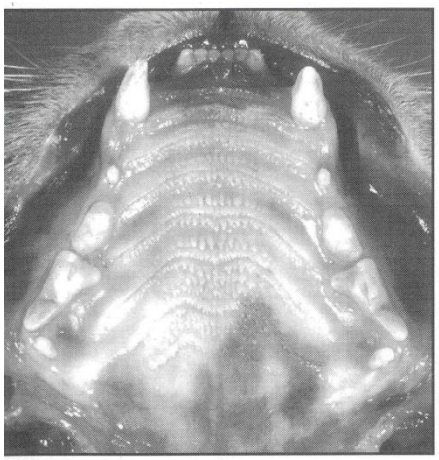
=> nowadays: 'omnivore dog dogma'

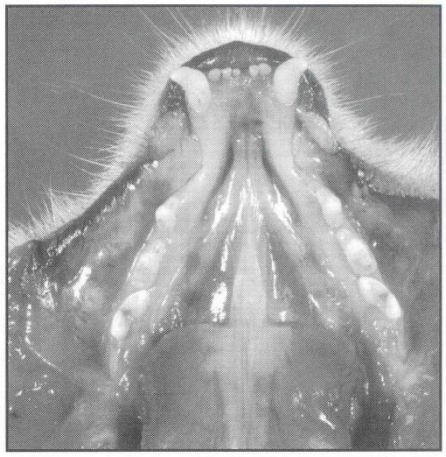
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Differences between dogs & cats









Cat: strict carnivore

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Differences between dogs & cats
Nutrients

- Nutrient requirements <-> prey
- Strict carnivores depend on nutrient from these prey
  - ↘ need for synthesis from precursors

- E.g. protein, arginine, taurine, arachidonic acid

vitamin A, niacine

CAT = TRUE CARNIVORE

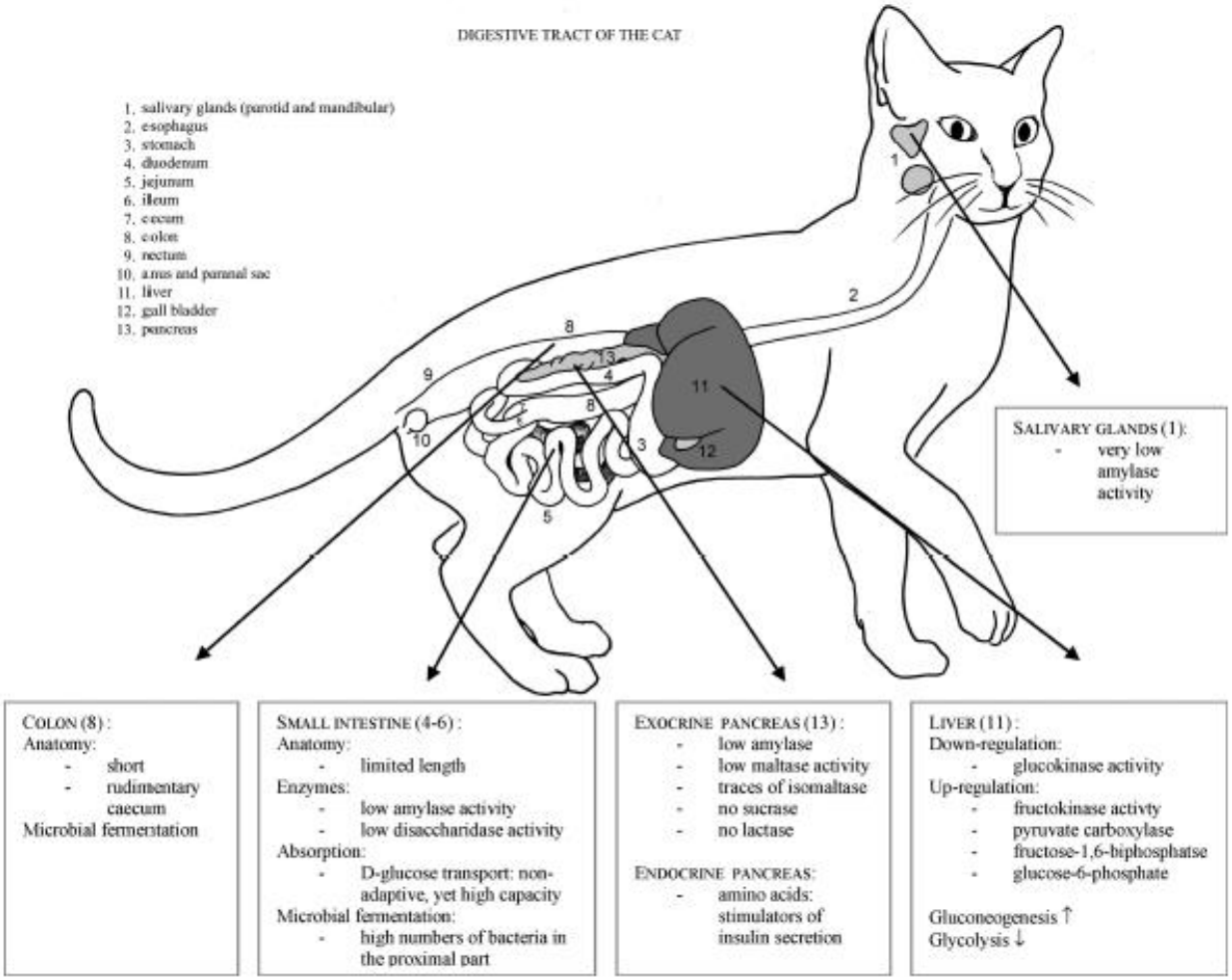


Figure 2 Physiologic adaptations of carbohydrate digestion in the feline gastro-intestinal tract.

Verbrugghe et al. 2012


Differences between cats (strict carnivore) & do
=> omnivorous dog dogma
<-> ancestors, carnivore ecology?
Canis familiaris, subspecies
Canis lupus

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Diet Wolf



- Ungulates but also small mammals, birds, reptiles, insects, fish
- Plant material (grass) in 32,6% of scats; though only 0,1-3%
- No intake of rumen content!

- **Wolves: carnivores with a very limited intake of vegetable material**

Bosch et al., 2015

Table 2. Data of dietary profiles of feral cats found in the literature (% of weight)

Dietary item‡	Study no.* 2	4	5	6	11	16	19	23† A	23† B	23† C	25	29† A	29† B	30	32	33	34
Mammals	84·5	81·0	9·8	93·1	87·2	96·7	84·0	86·7	62·3	85·9	66·9	80·5	69·6	76·0	85·4	88·3	90·5
Rodents	3·5	69·3	9·8	72·1	–	95·8	81·0	10·7	1·8	2·4	51·3	25·0	23·5	21·0	25·7	18·1	31·3
Rats	–	4·3	9·8	69·8	–	95·8	81·0	2·1	–	–	39·1	–	–	17·2	12·2	14·5	9·1
Mice	3·5	10·3	–	–	–	–	–	8·5	1·8	2·4	12·2	–	–	3·8	13·5	3·6	12·6
Voles	–	51·6	–	2·3	–	–	–	–	–	–	–	–	–	–	–	–	–
Others rodents	–	3·1	–	–	–	–	–	–	–	–	–	25·0	23·5	–	–	–	9·6
Rabbits	70·0	8·3	–	21·0	82·6	–	–	74·3	56·4	43·2	–	53·2	34·3	55·0	59·7	70·2	57·8
Insectivores	9·5	0·6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1·4
Other mammals	1·5	2·8	–	–	4·6	0·9	3·0	1·7	4·1	40·3	12·6	2·3	11·8	–	–	–	–
Birds	10·0	18·7	81·3	6·6	6·6	3·1	13·0	8·9	18·2	12·9	23·9	12·9	8·4	23·3	0·8	4·5	6·5
Reptiles/amphibians	1·0	0·1	–	0·2	4·7	–	2·0	0·5	2·1	0·2	–	1·8	14·1	–	13·6	7·1	2·0
Invertebrates	1·0	+	–	+	1·5	0·2	1·0	1·2	0·9	0·3	1·6	2·6	6·8	–	+	0·1	1·1
Fish	–	0·2	–	–	–	–	–	0·7	9·5	–	–	–	–	–	–	–	–
Carrion	–	–	8·9	–	–	–	–	2·0	6·9	0·7	7·4	2·2	1·1	–	–	+	+
Eggs	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plant matter	+	+	+	–	–	+	–	+	+	+	–	+	+	0·7	+	+	+
Human-linked foods	–	+	–	+	–	–	–	–	–	–	–	–	–	+	+	–	+
Unidentified	3·5	–	–	–	–	–	–	–	–	–	0·2	–	–	–	–	–	–

Dietary item‡	Study no.* 38	39	40	41	42	43	44	45	46	47	48	52	55	Mean	SEM
Mammals	85·4	77·5	99·5	89·2	90·0	74·5	83·5	85·1	72·8	92·6	89·4	54·0	1·8	77·5	4·0
Rodents	14·3	12·1	8·0	70·6	90·0	74·5	83·5	11·6	5·4	4·2	5·9	33·0	1·8	31·9	5·8
Rats	2·8	8·7	–	60·9	+	68·4	42·9	–	–	–	3·3	31·0	–	19·1	5·2
Mice	11·5	3·4	8·0	9·7	+	6·1	30·7	11·6	5·4	4·2	2·6	2·0	1·8	5·6	1·2
Voles	–	–	–	–	–	–	–	–	–	–	–	–	–	1·8	1·7
Others rodents	–	–	–	–	90·0	–	9·9	–	–	–	–	–	–	5·4	3·1
Rabbits	71·1	65·4	91·5	18·6	+	–	–	72·6	64·7	88·4	83·5	–	–	41·5	6·0
Insectivores	–	–	–	–	–	–	–	–	–	–	–	–	–	0·4	0·3
Other mammals	–	–	–	–	–	–	–	0·9	2·7	–	–	21·0	–	3·7	1·5
Birds	8·0	1·5	0·3	4·3	6·8	25·1	8·8	14·9	18·1	2·0	3·6	30·0	96·6	16·0	3·9
Reptiles/amphibians	5·9	20·9	0·1	6·3	2·6	0·2	5·6	–	8·3	0·9	6·6	3·0	–	3·7	0·9
Invertebrates	0·8	0·1	0·1	0·2	0·6	0·2	2·1	–	0·8	1·2	0·2	12·0	–	1·2	0·4
Fish	–	–	–	–	–	–	–	–	–	–	–	–	–	0·3	0·3
Carrion	+	–	–	–	–	–	–	–	–	0·2	–	+	1·3	1·0	0·4
Eggs	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
Plant matter	+	+	+	+	–	–	+	–	+	–	+	+	+	+	+
Human-linked foods	+	+	+	+	–	+	–	–	+	3·0	+	–	–	0·1	0·1
Unidentified	–	–	–	–	–	–	–	–	–	–	–	–	–	0·1	0·1

Plantinga et al., 2011

Table 3. Macronutrient composition of dietary ingredients of the feral cat diet

Dietary item	Energy (kJ ME/100 g DM)	DM (% as is)	DM (%)				References
			CP	EE	Ash	NFE	
Rats	1965	33·4	60·1	30·5	9·4	0·0	(128–131)
Mice	1812	33·1	59·1	24·5	11·3	5·1	(60,131–133)
Voles	1638	31·1	64·5	17·2	12·7	5·6	(60,132,134)
Other rodents*	1745	31·1	65·5	22·1	12·4	0·0	(60,132)
Insectivores†	1644	31·2	61·6	19·0	14·9	4·5	(132)
Rabbits	1748	26·1	63·9	22·3	12·5	1·3	(77,135)
Other mammals‡	1918	34·2	55·6	31·0	13·4	0·0	(134)
Birds§	1642	31·6	64·6	15·9	10·6	8·9	(134)
Reptiles/amphibians‖	1430	24·8	65·7	9·0	15·2	10·1	(77,78)
Fish¶	1870	25·5	69·1	24·1	6·8	0·0	(136)
Invertebrates**	1812	34·7	62·3	20·0	4·8	12·9	(44,134,137–139)

ME, metabolisable energy; CP, crude protein; EE, ethereal extract; NFE, N-free extract (100 – CP – EE –ash).
* Derived from four different squirrel species.
† Derived from moles.
‡ Derived from ten different species of bats and opossums.

Plantinga et al., 2011

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Nutrient profile

% Energy	Free roaming cat	Wolves
protein	52	54
fat	46	45
Carbs	2	1

Cat = strict carnivore <-> dogs/wolves: metabolic adaptations

Bosch et al., 2015, Hewson-Hughes et al., 2011; 2013; Plantinga et al., 2011

Wolf	Cat
Pack hunter	Solitary hunter
Big prey	Many small prey
Unregular	Regular meals
“Feast and famine”	
Metabolic adaptations: protein sparing! Synthesis of ‘essential’ nutrients	

Bosch et al., 2015

Consequence ‘feast –famine’ lifestyle

Famine	Feast
Protein sparing capacity	Preferential intake of organs
Decrease metabolic losses	Lever -> glucogen
Synthesis of ‘essential nutrients’: Arg, taurine, AA	Lever -> vitamin A Dogs more resistant to toxicity than cats

Bosch et al., 2015

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Nutrient profile & -preference

% Energy	Cat*	Free roaming cat	Wolves	Dogs*
protein	52	52	54	30
fat	36	46	45	63
Carbs	12	2	1	7

* preference



Optimal for health?

Bosch et al., 2015, Hewson-Hughes et al., 2011; 2013; Plantinga et al., 2011

Role of domestication?

1. Dog

- First domesticated animal, ~14000y ago
- Evolved from wolf
- Domestication => influence on social, cognitive traits but also type of food
- Very adjustable & depending on environment

=> Gene mutations -> starch digestibility

2. Cat

- Domesticated more recent -> 4000y ago

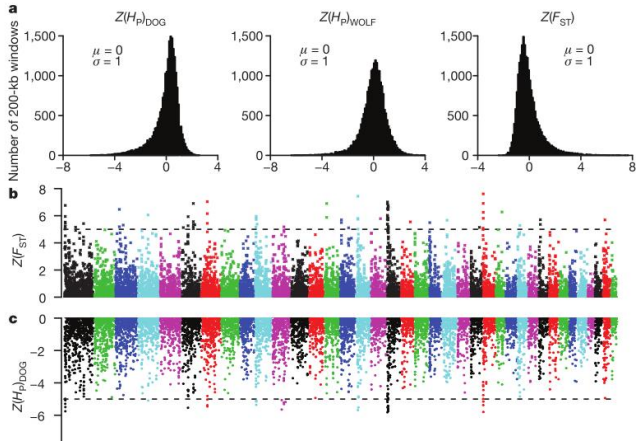
Buff et al., 2014

Role of domestication?

- Whole genome resequencing 12 wolves <-> 60 dogs, 14 breeds
- 10 genes: starch & fat metabolism

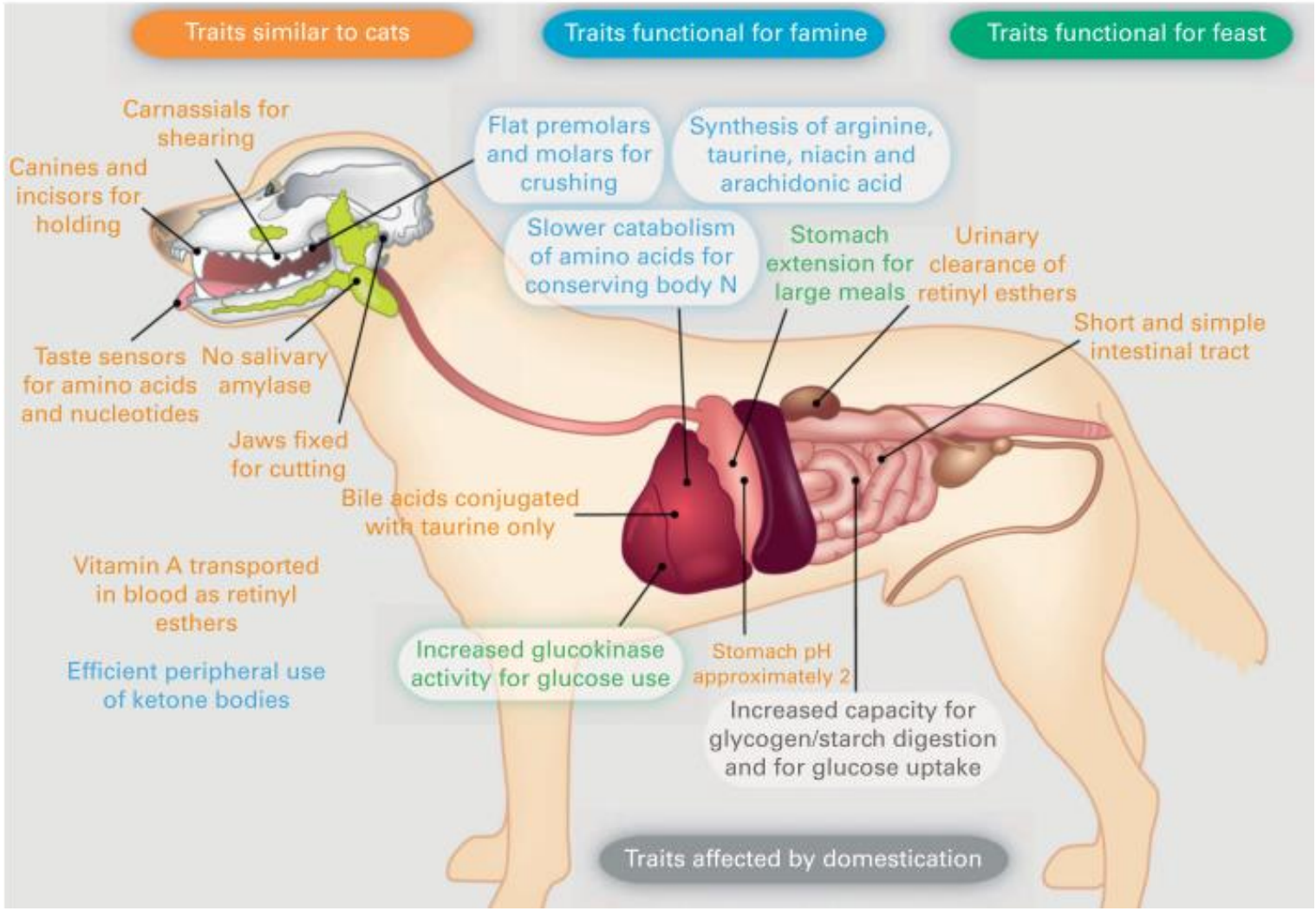
⇒ **Assumes starch digestion dogs > wolves**

⇒ **Important step in early domestication**



Axelsson et al., 2013

Nutrient intake in wild wolves



Bosch et al., 2015

Conclusion : omnivore dog dogma





- Cats: strict carnivores
- Wolves: carnivores with metabolic adaptations because of ‘feast-famine’ lifestyle
- Dogs : evolution due to domestication e.g. starch digestibility

=> **adapted carnivores**

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‘Wild diet’ compared to nutrient requirement of cats

Table 5. Recommended nutrient composition *v.* assessed nutrient composition of the ‘natural’ cat diet

	National Research Council[35]						
	Growth		Maintenance		Late gestation/peak lactation		Present study
Nutrient (MJ/ME)	Minimal	Recommended	Minimal	Recommended	Minimal	Recommended	Mean
Protein (g)	10·8	13·5	9·6	12·0	10·3	12·7	35·4
Fat (g)	–	5·4	–	5·4	–	5·4	12·9
Ca (g)	0·31	0·48	0·10	0·17	0·00	0·65	1·5
P (g)	0·29	0·43	0·08	0·15	0·29	0·45	1·0
K (g)	0·16	0·24	–	0·31	–	0·31	0·53
Na (g)	0·07	0·08	0·04	0·04	0·00	0·16	0·28
Mg (mg)	9·6	23·9	12·0	23·9	24·9	29·9	73·4
Fe (mg)	4·1	4·8	–	4·78	–	4·78	16·7
Cu (mg)	0·26	0·50	–	0·29	–	0·53	0·9
Zn (mg)	3·0	4·4	0·00	4·42	2·51	3·59	5·5

ME, metabolisable energy.

Plantinga et al., 2011

What is optimal?

Traditional commercial diets
Myths

Composition:
cereals (including 4% whole wheat), meat and animal derivatives (including 4% poultry), derivatives of vegetable origin, oils and fats, minerals.

Starch content

=> adult dog: 35-60%

- No minimum carbohydrate requirement (NRC, 2006)
- Optimal carbohydrate intake?
- Mean digestibility starch: 85%
- No proof for increase in Diabetes & Obesity



Axelsson et al. 2013: „The genomic signature of dog domestication reveals adaptation to a starch-rich diet"

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veterinary sciences

MDPI

Review

Cats and Carbohydrates: The Carnivore Fantasy?

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2 Laboratory of Animal Nutrition, Faculty of Veterinary Medicine, Ghent University, Heidestraat 19, Merelbeke B-9820, Belgium; Myriam.Hesta@ugent.be
* Correspondence: averbrug@uoguelph.ca; Tel.: +1-519-824-4120

Academic Editor: Jacquie Rand
Received: 28 June 2017; Accepted: 8 November 2017; Published: 15 November 2017

Abstract: The domestic cat's wild ancestors are obligate carnivores that consume prey containing only minimal amounts of carbohydrates. Evolutionary events adapted the cat's metabolism and physiology to this diet strictly composed of animal tissues and led to unique digestive and metabolic

Vet. Sci. **2017**, 4, 55; doi:10.3390/vetsci4040055

Traditional commercial diets
Myths

- Grains

1) Fillers, no nutritional value

Grains => carbs (75%); protein (6-10%), essential fatty acids (4-5%), fiber (7%)

Higher contents after treating grains

2) Low Quality

Control before, during and after production

3) Food allergy gluten allergy very rare

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Prevalence & risk factors for Obesity in dogs

Table 2
Selected reported prevalences of veterinary-diagnosed canine overweight and obesity

Reference	Geographic Location	n	Prevalence	Risk Factors and Associations
Kronfeld et al,[20] 1991	Veterinary Hospital of the University of Pennsylvania	3729	22.9%	Breed, middle age
McGreevy et al,[21] 2005	Veterinary practices in Australia	2661	41.1%	Middle age, neuter, breed, female, rural and semirural region
Lund et al,[12] 2006	US veterinary clinics	21,754	34%	Neuter, age, semimoist, canned, or homemade food, consumption of table scraps or commercial treats, breed, geographic region
Colliard et al,[22] 2006	National Veterinary School of Alfort teaching hospital (Paris, France)	616	38.8%	Neuter, female, age, breed, older or retired owner, homemade food
Weeth et al,[23] 2007	Veterinary Medical Teaching Hospital of University of California, Davis	14,670	36.4%	Neuter, breed
Courcier et al,[24] 2010	Veterinary practices in UK	696	59.3%	Frequency of snacks/treats, increasing owner age and lower income, hours weekly exercise
Corbee,[25] 2013	Show dogs in the Netherlands	1379	18.6%	Certain breed groups
Mao et al,[26] 2013	China	2391	44.4%	Noncommercial food, neuter, female, middle age, low activity, feeding more than once per day

Larsen & Villaverde, 2016

Prevalence & risk factors

Table 1
Selected reported prevalences of veterinary-diagnosed feline overweight and obesity

Reference	Geographic Location	n	Prevalence	Risk Factors and Associations
Scarlett et al,[13] 1994	Northeast US veterinary clinics	>2000	24%	Indoor living, inactivity, middle age, male, neuter, mixed breed, some dry foods
Russell et al,[14] 2000	London (UK) households	136	52%	Neuter, middle age, frequent treating, free feeding
Lund et al,[3] 2005	US veterinary clinics	8159	35%	Neuter, male, premium or therapeutic food, breed
Colliard et al,[15] 2009	National Veterinary School of Alfort teaching hospital (Paris, France)	385	26.8%	Male, neuter, owners underestimating BCS
Courcier et al,[16] 2010	Glasgow, Scotland	118	39%	Frequency of feeding, neutered status
Cave et al,[17] 2012	Households urban area (Palmerston North, New Zealand)	200	63%	Age, longer leg length, owners underestimating BCS
Courcier et al,[18] 2012	Great Britain veterinary clinics	322	11.5%	Neuter status, male, middle age
Corbee,[19] 2014	Show cats in the Netherlands	268	45.5%	Neuter status, breed

Larsen & Villaverde, 2016

Dietary risk factors for obesity

Box 2
Dietary factors associated with overweight or obesity in dogs and cats

- No association between diet type and obesity in cats.[15,18]
- Dry food as risk factor for development obesity in young cats.[17]
- Dietary fat content, rather than carbohydrate associated with obesity in cats.[19]
- Feeding free choice seems to increase the risk of obesity in cats.[15,16]
- An association between numbers of meals and snacks and obesity in dogs.[20]
- Feeding of table scraps associated with obesity in cats and dogs.[15,16,20,21]
- Cat or dog present when food is prepared.[15,16,20,21]
- 'Grocery store' dog foods positively associated with canine obesity.[18]
- 'Premium' cat foods positively associated with feline obesity.[5]

German, 2016

Box 3
Owners factors implicated in the development of overweight and obesity in dogs

- Lower average income for owners of overweight dogs,[18,22] but not cats.[23]
- Overhumanization of the dog by the owner is associated with obesity in dogs.[18]
- Cat used by owner as a human companion substitute.[23]
- Close observation of feeding behavior of the cat or dog.[18,23]
- Less time spent playing with cat.[23]
- Owner obesity positively associated with obesity in dogs[18] and cats.[23]
- Owners of obese cats less interested in preventive health[18,23]
- A stronger owner–animal bond is reported between obese cats and their owners.[14]

Dietary carbs are not a risk factor for obesity!



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Carbs in cat feed

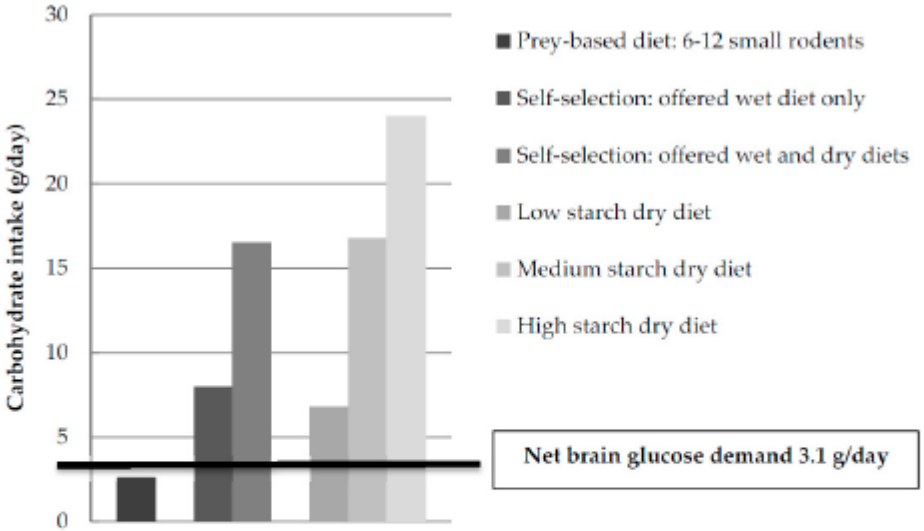


Figure 4. Carbohydrate intake following consumption of a prey-based diet (NFE 1–2%ME, carbohydrate intake presented is a calculated average of 6–12 small rodents per day including gut content, glycogen and glucose from glycerol) [1,48], following self-selection from only wet diets (NFE 12%ME) [50] or from diets with different texture and moisture content (NFE 11–21%ME [51], and following ingestion of dry diets with various starch levels (NFE 12%, 30% and 43%ME, respectively) [52] compared to the calculated net brain glucose demand [48].

Verbrugghe & Hesta 2017

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Dietary carbs as cause for feline diabetes?



Mouse: protein 55.8%, fat 23.6% , carbs 8.8%DS

Prey: carbs:1-2%ME

Hypothesed role of high carb diets?

Traditional diets: 20-40%ME



Overproduction Insuline => fat deposition

Higher demand of insulin by β-cells => amyloïdosis pancreas, exhaution of β-cellen

Incidence ↑ Obesity & type 2 diabetes ?

Carbs as cause of feline obesity & diabetes?

Table 2. Animal, lifestyle and dietary factors increasing the risk for feline obesity and diabetes mellitus.

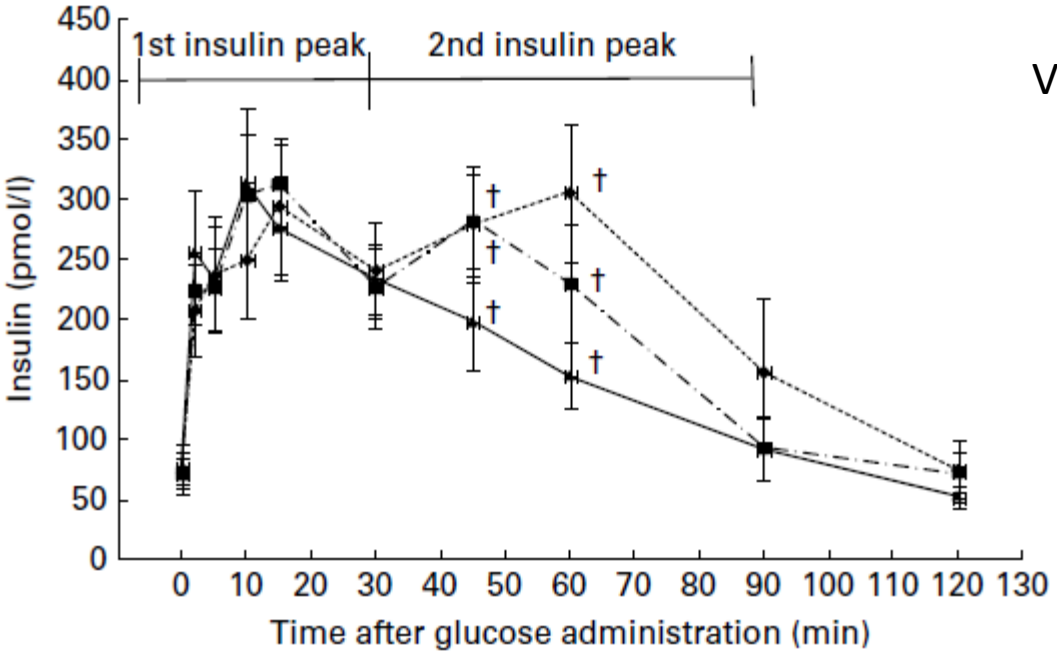
Factors Predisposing Cats to Obesity		Factors Predisposing Cats to Diabetes Mellitus
	Animal factors	
Mixed breed [69,89,101,108] Norwegian Forest, British Shorthair, Persian [109]	**Breed**	Tonkinese, Norwegian Forest, Burmese Russian Blue, and Abyssinian [110–115]
Middle age [69,89,101,108,116]	**Age**	Older than 7 years [112–115,117–119]
Male [69,89,101,108,116,120]	**Gender**	Male [102,110–113,115,117–120]
Neutered [69,89,101,108,116]	**Sexual status**	Neutered [111,118,119]
	Lifestyle factors	
Inactive cat [69,89,90,102]	**Physical activity**	Inactive cat [110,111,117,121]
Indoor confinement [69,89,102]	**Housing**	Indoor confinement [110,121]
	Dietary factors	
Dry food: No influence [69,86,90,100] Increased risk [89,101,102]	**Diet type**	Dry food: No influence [121] Reduced risk [117] Increased risk [11]
Free choice feeding: Increased risk [97,99] No influence [69,86,89,90,108]	**Feeding method**	Free choice feeding and greedy eating behaviour [110]
Homemade food, human foods and/or treats [98]	**Other dietary inclusions**	
Obese cats are up to four times more likely to develop diabetes mellitus [110,111,113,117–119,122]		

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Low carb diet in healthy cats



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Fig. 1. Insulin curve during intravenous glucose tolerance tests in healthy cats fed a low-protein (LP), a low-fat (LF) and a low-carbohydrate (LC) diet. Values were expressed as expressed as mean values with their standard errors. † Mean values tended to be different among test diets ($0{\cdot}05 < P < 0{\cdot}1$). --◆--, LC diet; - .■- ., LF diet; —▲—, LP diet.

Low carb diet in healthy cats

Table 3. Serum insulin concentrations during intravenous glucose tolerance tests in healthy cats fed a low-protein (LP), a low-fat (LF) and a low-carbohydrate (LC) diet

(Mean values with their standard errors)

	LP			LF			LC			
	Mean	SE	n^*	Mean	SE	n^*	Mean	SE	n^*	P
Basal insulin (pmol/l)	74·6	21·7	9	71·4	13·0	9	75·3	13·4	9	0·971
Insulin after 2 min (pmol/l)	256·1	50·9	8	224·0	28·6	7	208·3	24·0	9	0·510
Insulin after 5 min (pmol/l)	233·5	45·3	8	225·7	34·4	8	236·7	46·1	7	0·533
Insulin after 10 min (pmol/l)	314·0	63·2	8	303·3	51·1	9	319·9	49·7	9	0·239
Insulin after 15 min (pmol/l)	276·7	43·1	6	313·1	34·[illegible]	9	294·7	57·1	9	0·901
Insulin after 30 min (pmol/l)	233·9	29·8	8	225·[illegible]	33·[illegible]	9	241·3	40·3	9	0·339
Insulin after 45 min (pmol/l)	198·0	38·9	8	283·[illegible]	39·2	9	238·2	48·1	9	0·069
Insulin after 60 min (pmol/l)	153·1	26·9	8	229·8	50·0	9	306·0	57·5	9	0·051
Insulin after 90 min (pmol/l)	91·7	21·1	8	9[illegible]·6	24·7	9	156·3	61·6	9	0·251
Insulin after 120 min (pmol/l)	5[illegible]	8·3	7	7[illegible]·2	16·4	9	74·8	25·4	8	0·538
AUC_{ins} (pmol/l × 120 min)	19139[a]	2380	8	23955[b]	3325	8	26356[b]	4022	9	0·019
Time 1st insulin peak (min)	5·6	1·1	8	7·6	1·9	9	9·6	2·2	9	0·[illegible]
Time 2nd insulin peak (min)	6[illegible]	6·7	8	44·4	4·8	9	52·5	7·5	8	0·060
Height 1st insulin peak (pmol/l)	328·6	56·7	8	295·6	38·0	9	301·4	54·5	9	0·645
Height 2nd insulin peak (pmol/l)	283·4	48·8	8	324·3	50·2	9	364·5	62·4	9	0·436
Basal SI	19·9	5·4	9	18·9	3·2	9	19·0	3·0	9	0·967
AUC_{ins}/AUC_{gluc}	20·9	3·3	8	24·0	3·0	8	24·4	3·4	9	0·386
HOMA	12·6	3·9	9	12·1	2·4	9	13·5	2·7	9	0·905
QUICKI	0·45	0·03	9	0·43	0·01	9	0·42	0·02	9	0·386
Bennett index	1·13	0·14	9	0·99	0·05	9	0·99	0·09	9	0·349

AUC_{ins}, area under the curve for insulin; AUC_{ins}/AUC_{gluc}, ratio of area under the insulin to glucose curve; HOMA, homoeostasis model assessment; QUICKI, quantitative insulin sensitivity index.

[a,b] Mean values within a row with unlike superscript letters were significantly different ($P<0·05$).

* $n < 9$ is caused by missing values.

Cat = strict carnivore => insuline response after absorption of aminoacids

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Conclusion

- Different life style in wild felines versus wolves
- Effect of domestication in dogs
- Cats: strict carnivores <-> dogs adapted carnivores
- Higher dietary carbs in traditional diets do not cause obesity & diabetes