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THE PIG AS A MODEL FOR HUMAN NUTRITION

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PIGS AND PEOPLE

Economic and Social Relationships

Clifford Pope (113) in his essay "On the Natural Superiority of Pigs" points out that "Man's association with the pig goes back tens of thousands of years and has been an intimate one since domestication took place in Europe and Asia some 7000 years ago." Pope suggests that "If the domestic pig had its way, it would replace the dog as man's best friend instead of his best source of protein."

The modern domestic pig is descended from the European wild pig *Sus scrofa* and the East Indies pig *Sus vittatus*. Domesticated pigs were brought to the New World by the Spanish explorers (Columbus to Desoto) and later by

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the colonists from England. By 1850, Cincinnati was the pork-packing center of the US and was known throughout the country as "Porkopolis." Since then, modern pig production in the US has moved further west and centers in the corn belt states. Around the world, pigs are produced for pork predominantly in (*a*) temperate climates, where (*b*) inexpensive, high-energy feedstuffs such as grains are available, near (*c*) large human populations who comprise the market for pork, and where there is (*d*) advanced technology in pork production (35).

Modern pork production (106) is a highly sophisticated agribusiness in which pigs are bred, born, and reared in environmentally controlled, confinement facilities, fed on computer-formulated diets based on grain (supplying most of the energy and some amino acids), with some soybean meal (supplying most of the amino acids and some energy), and fortified with appropriate levels of minerals and vitamins. This produces market pigs weighing 100 kg at five or six months of age and yielding a 75-kg carcass with a minimum of fat and 40 to 45 kg of muscle.

The pig is very efficient at converting feed to gain (feed/gain = about 3 to market weight). The product marketed is a high-quality protein with a minimum of fat for the human diet and also is an excellent source of the B vitamins and trace elements. In the US and Europe, annual per capita consumption of pork is about 30 kg. Worldwide per capita consumption of pork is about 10 kg annually. Also, worldwide there are about 750 million pigs marketed for about 4.5 billion people or one pig for six people. Marketing of pigs in the state of Iowa alone yields about $2 billion annually.

Comparative Biology

The biology of the pig is not unlike that of the human and other mammals in many respects (107). The pig has been used as a model for research in cardiovascular physiology, obesity, stress, dermatology, teratology, toxicology, immunology, behavior, hemodynamics, renal physiology, experimental surgery, gastroenteritis, diabetes, drug metabolism, and perinatology, as well as many aspects of nutrition (24, 139). Pond & Houpt (107) point out that the pig is similar to humans in dental characteristics, renal morphology and physiology, eye structure and visual acuity, skin morphology and physiology, cardiovascular anatomy and physiology, and digestive anatomy and physiology.

The size and body conformation of the pig can be changed relatively rapidly because of the high degree of heritability of body conformation characteristics, a relatively short generation interval, and high prolificacy. Thus, miniature pigs were developed initially by the Hormel Institute of the University of Minnesota (32) using classical genetic selection procedures to provide a smaller animal for biomedical research. Since then others have developed other strains of miniature pigs (33, 42).

Similarities and differences in thermoregulation and metabolism of newborn pigs and human infants are covered in a book by Mount (94). Both experience a drop in body temperature at birth followed by a rise; both have little thermal insulation, and the metabolic rates of both increase in the first days following parturition. The pig has a lower birth weight, more rapid growth rate, higher body temperature, higher metabolic rate, and lesser fat reserve than the human baby (21). Hakkarainen has published an extensive study on developmental changes of protein, RNA, DNA, lipid, and glycogen in various tissues of the piglet (46).

A summary (Table 1) of some of our studies on changes in the hematology of prenatal and postnatal swine is presented to provide normal values for healthy pigs. At many similar developmental points, the values for pigs are similar to those for humans. There are some distinct differences particularly in serum proteins at parturition. More extensive studies of swine hematology are reported by others (120, 140).

Over 60 years ago, Moulton (93) published a paper in which he concluded that mammals reach chemical maturity at different ages, but these ages are a fairly constant relative part of the total life cycle. Some of his data comparing man and pig are presented in Table 2. The portions of total life to reach chemical maturity (4.4% for man and 4.6% for pigs) are nearly identical, and the chemical compositions of fat-free body tissue (water, protein, and ash) at common stages of life are similar for man and pigs.

Comparative Nutrition

DIGESTION AND METABOLISM In their book, *The Biology of the Pig,* Pond & Houpt (107) state "In its nutrient requirements, the pig resembles the human in more ways than any other nonprimate mammalian species. This is due to the physiological and anatomical similarity of the digestive tract of the pig and man. This similarity provides a basis for the use of the pig in many human nutritional studies. Among the uses of the pig in this area are studies of atherosclerosis, calorie-protein malnutrition, and nutrient absorption and metabolism."

There are some excellent recent books on digestion and absorption in pigs, including *Digestion in the Pig* by Kidder & Manners, 1978 (58); *Current Concepts of Digestion and Absorption in Pigs,* edited by Low & Partridge, 1980 (68); and *Comparative Nutrition of Fowl and Swine: The Gastrointestinal Systems* by Moran, 1982 (92). Hakkarainen (46) has published his extensive studies on developmental changes in metabolism of the piglet with special emphasis on protein synthesis. Because of space limitations we do not present a detailed discussion of digestion, absorption, and metabolism here; readers are referred to these works for this detailed information. Recent reviews have been published on control of ingestive behavior (11, 54), gastrointestinal responses to food intake and dietary fiber (105), digesta

Table 1 Swine hematology

I. Cellular components

A. Erythrocyte population, size and hemoglobin concentration

	RBC[a] count (10^6/mm^3)	Reticulocytes (% of RBC)	PCV[b] (%)	MCV[c] (μ^3)	Hgb[d] (g/dl)	MCH[e] (10^{-12}g)	MCHC[f] (%)
1. Prenatal[g]							
a. 51 days	2.0	1.6	24	117	6.4	31	27
b. 72 days	3.4	0.4	30	91	8.7	26	29
c. 93 days	4.0	0.9	32	80	2.6	22	29
d. newborn	5.8	0.5	39	67	12.1	21	31
2. Postnatal[h]							
a. birth	6.2	0.6	40	65	12.5	20	31
b. 2 days	5.5	1.6	33	60	10.0	18	30
c. 7 days	5.0	3.9	24	64	9.8	18	29
d. 3 weeks	5.8	1.4	35	58	10.4	18	29
e. 5 weeks	6.0	1.6	32	52	9.4	15	29
f. 2 months	6.1	4.0	34	51	10.8	17	31
g. 4 months	6.8	1.2	37	54	12.2	20	33
h. 6 months	6.9	1.3	39	59	12.4	20	33
i. 1 year	6.9	6.3	39	56	13.2	20	34
j. 2 year	6.5	6.3	38	59	12.8	20	34

B. Leukocyte population and differentiation

	WBC count (10^3/mm^3)	Lymphocytes (%)	Monocytes (%)	Neutrophils (%)	Basophils (%)	Eosinophils (%)
1. Prenatal[g]						
a. 51 days	1.4	--	--	--	--	--
b. 72 days	2.2	--	--	--	--	--
c. 93 days	2.8	--	--	--	--	--
d. newborn	5.2	38	0.7	61	0.1	0.1
2. Postnatal[i]						
a. birth	5.7	28	1	71	0	0
b. 2 days	5.7	42	7	49	1	0
c. 7 days	7.7	53	4	41	1	1
d. 3 weeks	7.1	80	3	16	0	1
e. 5 weeks	11.8	65	5	28	1	2
f. 2 months	14.9	64	4	28	1	2
g. 4 months	20.4	63	7	24	1	6
h. 5 months	18.8	58	7	30	1	4

Table 1 *(continued)*

II. Plasma or serum components

A. Serum proteins and electrophoretic distribution

	Total serum protein (g/dl)	γ-globulin (%)	β-globulin (%)	α-globulin (%)	Albumin (%)
1. Prenatal[g]					
a. 51 days	2.8	9	35	33	23
b. 72 days	2.2	11	27	40	22
c. 93 days	2.5	9	23	51	17
d. newborn	2.9	11	20	48	21
2. Postnatal[j]					
a. birth	2.2	6	16	61	17
b. 6 hour	3.7	32	24	35	9
c. 12 hour	5.7	43	24	24	8
d. 24 hour	5.2	46	21	24	9
e. 2 days	5.3	41	21	23	15
f. 7 days	4.8	25	18	25	32
g. 3 weeks	4.8	10	18	24	48
h. 5 weeks	4.8	8	19	26	46
i. 2 months	5.4	14	16	29	41
j. 4 months	6.8	23	13	23	41
k. 6 months	6.8	19	13	19	49
l. 1 year	7.5	16	13	18	53
m. 2 years	7.8	18	13	17	52

B. Serum mineral concentration

	mg/dl					μg/dl		
	Ca	P	Na	K	Mg	Cu	Zn	Fe[l]
1. Postnatal[k]								
a. birth	11	5	356	20	3.4	27	60	90
b. 2 days	9	7	353	18	2.4	58	102	5800
c. 7 days	11	10	356	21	4.2	140	141	180
d. 2 weeks	11	11	353	20	4.4	195	100	205
e. 3 weeks	12	10	336	20	3.5	198	54	177
f. 5 weeks	11	8	342	19	3.0	153	61	228
g. 2 months	12	8	344	21	3.0	183	108	--
h. 4 months	11	8	360	21	2.8	187	94	--
i. 5 months	11	7	355	20	3.0	190	88	--

(continued)

Table 1 *(continued)*

III. Blood, plasma and cellular volumes	Body weight (BW) (kg)	Blood volume (ml/100 g BW)	Plasma volume (ml/100 g BW)	Cell volume (ml/100 g BW)
1. Postnatal[m]				
a. birth	1.4	8.6	5.4	3.2
b. 6 hours	1.6	9.4	6.2	3.2
c. 12 hours	1.4	9.9	6.5	3.4
d. 24 hours	1.6	9.8	6.7	3.1
e. 2 days	1.8	9.6	7.0	2.6
f. 5 days	2.4	9.7	6.7	3.0
g. 8 days	3.0	9.5	6.5	3.0
h. 2 weeks	5.0	8.2	5.2	3.0
i. 5 weeks	9.4	7.5	5.0	2.5

[a] Red blood cell.
[b] Packed cell volume.
[c] Mean corpuscular volume.
[d] Hemoglobin.
[e] Mean corpuscular hemoglobin.
[f] Mean corpuscular hemoglobin concentration.
[g] Reference 148.
[h] Reference 75.
[i] Reference 144.
[j] Reference 74.
[k] Reference 143.
[l] Reference 64.
[m] Reference 116.

Table 2 Age and chemical development of people and pigs (93)

	Man	Pig
Length of gestation (days)	285	114
Approximate length of life (years)	80	20
Age at chemical maturity (days)	1285	270–420
Total life at chemical maturity (%)	4.4	4.6
Composition at birth (fat-free basis)		
Water (%)	82	82
Protein (%)	14	13
Ash (%)	3	3
3 months (fat-free basis)		
Water (%)	81	77
Protein (%)	16	19
Ash (%)	3	4
Maturity (fat-free basis)	(33 yr)	(3 yr)
Water (%)	69	72
Protein (%)	21	23
Ash (%)	9	4

movement (66), and the use of reentrant ileocecal cannulas to study protein digestion and bile acid metabolism (19). Measures of the size and capacity of the digestive tract for pigs from birth to maturity are presented in Table 3. While the pig is primarily a nibbler under ad libitum feeding conditions, it is apparent from the data in Table 3 that the pig has the digestive capacity to function as a meal eater as well.

NUTRIENT REQUIREMENTS As one compares the nutrient requirements of the human (100) and the pig (101), he is impressed with the similarity between the two species in infancy, growth, reproduction, and lactation (Table 4). Such a comparison also calls attention to the need to establish requirements of the human for the individual amino acids, for pantothenic acid, biotin, choline, and for several of the inorganic elements.

THE PIG AS MODEL

Maternal and Fetal Nutrition

Minimum dietary nutrient requirements of sows during pregnancy and lactation have been established (7, 101) and recently reviewed (108). Like humans, pigs do not have a dietary requirement for protein per se in the diet but do have minimum dietary requirements for essential or indispensible amino acids (same ones as for humans) along with an adequate amount of nonessential amino nitrogen from various dispensible amino acids. However, in practical diets for sows nearly all of the amino nitrogen is supplied by proteins of

Table 3 Mean weights and capacities of the stomach and weights, capacities, and lengths of the intestines of pigs of different age groups [from Kvasnitskii (65) in Kidder & Manners (58)].

		Stomach		Small intestine			Large intestine		
Bodyweight (kg)	Age (d)	Weight (g)	Volume (l)	Weight (g)	Volume (l)	Length (m)	Weight (g)	Volume (l)	Length (m)
1	1	4.5	.02	40	.1	3.8	10	.04	.8
2	10	15	.07	95	.2	5.6	22	.09	1.2
3	20	24	.21	115	.7	7.3	36	.1	1.2
18	70	232	1.8	996	6.0	16.5	458	2.1	3.1
32	115	360	2.5	1,180	10.7	18.0	714	6.6	4.3
69	208	685	3.2	1,670	13.3	18.8	1,380	11.7	5.4
103	255	754	3.4	1,530	14.1	18.8	1,280	10.1	5.0
152	380	980	3.6	2,510	20.6	23.7	2,010	15.7	6.8
156	428	844	4.6	2,323	19.1	22.4	2,184	18.1	6.1
154	449	980	5.2	2,310	17.4	21.2	1,970	17.2	6.3
270	4 years	1,430	12.7	1,998	22.6	22.9	2,790	25.6	7.5

Table 4 Comparison of recommended daily allowances (RDA) in human diet and daily nutrient requirements (DNR) of pigs fed ad libitum except during pregnancy

	Human RDA[a]					Pig DNR[b]				
	Infant	Child	Adolescent	Preg.	Lact.	Infant	Weanling	Adolescent	Preg.	Lact.
Age	6 mo.	4-6 yr	11-14 yr	--	--	0-3 wk	3-6 wk	4-6 mo	1-4 yr	1-4 yr
Weight, kg	6-9	20	45	--	--	1-5	5-10	60-100	150-200	
Protein, g	13-20	30	45	76	66	67.5	100	390	216	618
Lysine, g	?	?	?	?	?	3.2	4.8	17.1	7.7	27.6
Methionine, g	?	?	?	?	?	1.9	2.8	9.0	4.1	17.1
Tryptophan, g	?	?	?	?	?	0.5	0.8	3.0	1.6	5.7
Vitamin A, IU	420	500	1,000	1,000	1,200	550	1,100	3,900	7,200	9,500
Vitamin D_3, IU	400	400	400	600	600	55	110	375	360	950
Vitamin E, IU	3	5	8	10	11	2.8	5.5	33	18	47.5
Vitamin C, mg	35	45	50	80	100	0	0	0	0	0
Thiamin, mg	0.3	0.9	1.4	1.4	1.5	0.33	0.65	3.3	1.8	4.8
Riboflavin, mg	0.4	1.0	1.6	1.5	1.7	0.75	1.5	7	3.6	14.2
Niacin, mg	6	11	18	5.5	18	5.5	11	30	18	47.5
Pantothenic acid, mg	?	?	?	?	?	3.3	6.5	33	21.6	57
Vitamin B_6,mg	0.3	1.3	1.8	2.6	2.5	0.38	0.75	3.3	1.8	4.8
Folacin, mg	30	200	400	800	500	150	300	1,800	1,100	2,800
Biotin, mg	?	?	?	?	?	0.03	0.05	0.3	0.2	0.5
Vitamin B_{12}, µg	0.5	2.5	3.0	4.0	4.0	5.5	11	33	27	71
Choline, mg	?	?	?	?	?	275	550	1,200	2,250	5,940
Calcium, mg	360	800	1,200	1,200	1,200	2,300	4,000	15,000	13,500	35,600
Phosphorus, mg	240	800	1,200	1,200	1,200	1,800	3,000	12,000	10,800	23,800
Magnesium, mg	50	200	400	450	450	100	200	1,200	700	1,900
Sodium, mg	?	?	?	?	?	250	500	3,000	2,700	9,500
Potassium, mg	?	?	?	?	?	1,800	1,300	5,100	3,600	4,500
Chlorine, mg	?	?	?	?	?	330	700	3,900	4,500	14,200
Iron, mg	10	10	18	40-70	40-70	38	70	120	144	380
Zinc, mg	3	10	15	20	25	25	50	150	90	238
Iodine, µg	40	90	150	175	200	40	70	400	250	660
Copper, mg	?	?	?	?	?	1.5	3	9	9	24
Manganese, mg	?	?	?	?	?	1	2	6	18	48
Selenium, µg	?	?	?	?	?	40	80	300	270	480

[a] NRC (100).
[b] NRC (101).

natural feedstuffs. With protein at 12% of the diet for pregnancy and 13% for lactation, all of the essential amino acid requirements are met by a corn-soybean meal diet. Essential amino acids account for about 35% of the protein in the pregnancy diet and 40% of that in the lactation diet (108).

Daily intake of 1800 g of a 12% protein corn-soybean meal type diet during pregnancy is adequate to meet the daily requirements for metabolizable energy (5760 kcal) and the essential amino acids. To meet the minimum requirements of energy (13,000 to 18,000 kcal ME/day) and amino acids for lactation, the sow should be allowed maximum voluntary intake of a 13% protein, corn-soybean meal type diet. Most efficient utilization of dietary energy and amino acids for productive purposes (anabolism) occurs during lactation when the demands are greatest (118). Pregnancy gives rise to appreciable extrauterine anabolism and this plus in utero development of the products of conception and a modest gain in bodyweight is accomplished on what is a maintenance diet for the nonpregnant sow (118). These phenomena, with the mechanisms presumably hormonal in origin, still require clarification.

During pregnancy the sow effectively buffers the developing fetus against protein and amino acid restriction (108). Moderate protein restriction during gestation affects subsequent milk production more adversely than it affects fetal development. Amino acid balance of low-protein gestation diets is important for proper fetal development. Atinmo et al (8–10) showed that the fetal growth suppression induced by maternal protein restriction of sows is associated with increased circulating levels of growth hormone and decreased levels of thyroxine and insulin in progeny during postnatal life. Normal patterns of circulating prolactin and growth hormone concentrations during fetal and postnatal growth of pigs have been described (61).

While both energy and amino acid restriction in diets of sows can influence fetal and neonatal growth, prolonged inanition of pregnant sows has minimal effects on embryonic, fetal, and neonatal survival (6, 47) and on postweaning growth and reproduction of female progeny (48). Maintenance of uterine blood flow during starvation was suggested as the physiologic adjustment that allowed normal fetal development (108). Pregnancy can be maintained in primiparous sows fed one third the recommended energy intake (2000 kcal DE/day); fetal weight, but not number of live fetuses, is reduced at 84 and 106–112 days (109).

Hausman et al (49) have studied various aspects of adipose tissue development in the fetus and have proposed the fetal pig model to identify specific factors responsible for adipocyte abnormalities of obesity.

Infant Nutrition

Baby pigs have a tremendous ability to grow during the typical nursing period from birth to 3–6 weeks of age. In the first 6 weeks of life the baby pig may

increase its birth weight by 1000% (from 1,200 to 12,000 g). By contrast, the human infant increases its birth weight by about 50% (from 3400 to 5000 g) during this same 6-week period (4). Because the baby pig grows so rapidly, it has more stringent nutritional requirements than the baby human (21). The baby pig may be weaned immediately after birth to an evaporated milk diet under germ-free conditions (89) or to the same diet in a conventional environment after consuming its mother's colostrum for 12 to 24 hours.

We weaned baby pigs from their mother at one to two days of age to a semipurified diet consisting of vitamin-free casein, glucose monohydrate, lard, and minerals and vitamins. This diet was stirred into water and homogenized at 200,000 g/cm^2 as a semisynthetic homogenized milk. We were then able to assay, through growth and biochemical measures, the dietary requirements of the baby pig for the individual vitamins (50, 76–79, 132) and inorganic elements (52, 80–83, 103, 126, 145). After the initial studies with the B vitamins and iron, we changed the form of the diet from a homogenized milk to a similar semipurified diet in a dry meal form. By incorporating 5% of α-cellulose into this dry diet we had a test diet that gave good growth rate of baby pigs fed ad libitum in individual cages. This enabled us to do element balance studies (28, 44, 51, 84–86) utilizing casein, soybean, and egg proteins (87, 88).

Others have used similar diets with artificial rearing systems to study the utilization of different dietary proteins (111, 147, 151) and energy sources (1, 14, 26, 124, 128). Similar systems have been used to evaluate infant formulas and milk substitutes (111, 121, 122) and to assess diets for rehabilitation of infants from protein-calorie malnutrition (110).

Pond et al (112) and Widdowson (153) have fed protein-deficient or energy-deficient diets to baby pigs as models for the human infant conditions of kwashiorkor and marasmus. Tumbleson and coworkers (141, 142) examined many hematological parameters related to malnutrition of miniature baby pigs. Young pigs have also been used as models for infant total parenteral nutrition studies (23, 43).

Carbohydrate and Lipid Metabolism

The newborn pig has very little body lipid but does have a limited energy reserve as glycogen in liver and muscle. Glycolytic capabilities are well developed at birth and this glycogen reserve rapidly disappears, particularly with cold stress and starvation, and the neonatal pig becomes hypoglycemic. This drop in glucose can be reversed by providing supplemental heat and food. Typically, the nursing pig obtains milk hourly from the dam and can maintain an adequate blood glucose level from milk lactose and fat. Gluconeogenesis capabilities develop quickly in the postnatal pig (20, 70, 71). The newborn pig has low blood and liver carnitine levels, but extremely high

levels of colostrum and milk quickly alleviate this deficiency (56). Fatty acid oxidation is not a limiting capability of the one-day-old pig (91).

Mersman (72) recently reviewed many facets of carbohydrate and lipid metabolism in pigs. Only a few of these are discussed here.

Waterman et al (149) fed diets containing fructose or glucose to rats, chicks, and pigs. Plasma triglyceride levels were elevated in rats but not in chicks or pigs fed diets containing fructose. The rate of fatty acid synthesis in rat liver but not in chick liver was elevated when fructose-containing diets were fed. Conversely, the rate of fatty acid synthesis in rat adipose tissue but not in pig adipose tissue was depressed when fructose-containing diets were fed. These results indicate that there are species-specific and organ-specific metabolic responses to various dietary carbohydrates.

Lipogenesis is markedly depressed as dietary fat level is increased in the diet of young pigs (2). Dietary tallow depressed adipose tissue lipogenesis in pigs to a greater extent than did the same dietary level of safflower oil (150). Activities of pentose pathway dehydrogenases and malic enzyme were depressed in adipose tissue homogenates of pigs fed high-fat diets (3).

In a study in which a low-fat, plant protein control diet and high-fat diets with either animal protein or plant protein containing either a saturated fat (sat) or a polyunsaturated fat (puf) were fed to pigs, plasma cholesterol levels at 90 kg were as follows: control, 89 mg/dl; plant/sat, 158 mg/dl; plant/puf, 111 mg/dl; animal/sat, 205 mg/dl and animal/puf 169 mg/dl. Both type of dietary protein and type of dietary fat had significant effects upon plasma cholesterol levels. Percentages of plasma lipoproteins as high density lipoprotein (HDL) were 29, 43, 67, and 50, respectively. The type of dietary protein had a significant effect; pigs fed animal protein diets had higher HDL values (38). Exercising pigs reduced plasma cholesterol 16%, and the percentage of cholesterol associated with HDL increased 33% compared to nonexercised pigs (39). Meal frequency (1 vs 4 meals/48 hr) did not influence glucose tolerance or plasma glucose, cholesterol, or triglyceride levels. Pigs fed less frequently (same total intake) exhibited elevated malic enzyme activity in adipose tissue (117).

Serum cholesterol of pigs was reduced by feeding propionate (135), with cholesterol shifting from the serum to the tissue pool. Dietary cellulose reduced both serum and liver cholesterol in pigs (37).

Amino Acid Metabolism

A recent review by Benevenga (15) argued that the knowledge obtained from amino acid metabolism studies in pigs was applicable to human nutrition. His studies (16) have demonstrated that either the 10-kg pig or the 90-kg pig adapts to a high-protein diet (63% crude protein) as readily as rats (5). The half-lives of liver protein in rats (133) and pigs (17) were similar (about 3.5 days). Their studies with marginally B_6-deficient pigs (127) showed promise

of a realistic model for the study of homocystinuria. The alternative of transsulfuration (transamination) is a pathway of methionine catabolism in both pigs and primates (18). Pigs and primates differ in their ability to utilize D-methionine (129). Primates utilize very little D-methionine, while neonatal miniature pigs utilize D-methionine about one half as efficiently as L-methionine.

Garlick et al (41) estimated rates of protein synthesis in 75-kg pigs and compared these with the rate of protein synthesis in 77-kg humans and 100-g rats. When protein synthesis was expressed in relation to resting metabolic rate (g/kcal), the results across species were nearly identical. As a percentage of total body synthesis, muscle protein synthesis in the pig (42%) is twice that seen in the rat (19%). Recently, Mulvaney et al (95) estimated rates of fractional protein synthesis (FSR), fractional protein breakdown (FBR), and fractional protein accretion or growth rates (FGR) of longissimus dorsi (LD), semitendinosus (ST), and brachialis (BR) muscles in 22-kg and 45-kg male pigs. FSR was approximately 20% lower for pigs at 45 kg than for pigs at 22 kg. At 22 kg, FGR for LD, ST, and BR were 0.7, 2.4 and 1.7% per day, respectively, and at 45 kg were 1.7, 1.9 and 0.7% per day, respectively. FBR (FSR − FGR) was 44, 16, and 8% lower for LD, ST, and BR muscles, respectively, at 45 kg than at 22 kg. Thus, rates of both protein synthesis and breakdown were relatively greater for the younger pig. The proportion of protein retained was approximately 28% of that synthesized by pigs at either weight. Garlick et al (41), Mulvaney et al (95), and Benevenga (15) all point out that since individual skeletal muscles differ in their turnover rates during growth and development, selection of a muscle for such studies is critical. In another study (63) it was found that total RNA increased linearly in BR and ST of male pigs as body weight increased from 105 to 145 kg.

Studies of the metabolism of monosodium glutamate in both pigs (130) and humans (131) have been conducted. Recent studies (29) have shown that supplemental carbohydrate in the diet decreased plasma glutamate levels, probably by increased metabolism in the intestine.

In amino acid nutrition of pigs the concept of the ideal protein for the functions of growth, reproduction, and lactation has been useful in expressing individual amino acid requirements. Pigs of different weight, sex, and breed would require different amounts of the ideal protein but the quality of the protein would be the same in each case for a common function (7, 27, 40, 69). Other studies have provided knowledge of the availability of dietary amino acids from natural and synthetic sources (12, 119, 134), which enables one to formulate diets very accurately.

Vitamin and Mineral Nutrition

Much of the exciting research with vitamins in recent years has involved the elucidation of metabolic roles of fat-soluble vitamins as exemplified in a

recent review of vitamin D (34). Many of the vitamin A studies with swine have defined dietary requirements for various stages of life-cycle nutrition and retinol potency of β-carotene in meeting this requirement (7, 101). On the basis of hepatic retinol storage it was determined that the retinol potency of all-*trans*-β-carotene (50, 146) and corn carotenes is about 250 IU per mg.

Plasma retinol and β-carotene levels elevated in gilts by weekly injections (25) led to increased amounts of uterine-specific proteins that were found (13) to be important in embryonic development. Increasing plasma retinol and β-carotene levels reduced embryonic mortality and resulted in heavier litters at birth and weaning (22). Concentrations of plasma immunoglobulins were higher in piglets nursing the injected gilts than in piglets nursing the noninjected gilts.

With the establishment of selenium (Se) as a nutrient in 1957 (123), it was recognized that many of the lesions observed in controlled studies of vitamin E and Se deficiencies were similar. Use of unsaturated fat in swine diets was responsible for much of the naturally occurring vitamin E and Se deficiency problem in Scandinavia (102). Cases of vitamin E–Se deficiency lesions were observed in the US in pigs fed low-fat, corn-soybean meal diets (73, 137). Researchers in Britain (104) and Scandinavia (136) demonstrated a low tolerance of vitamin-E–Se-deficient baby pigs to intramuscular injections of iron dextran, but in the US lesions could be produced only with massive injections of iron dextran (750 mg Fe/kg).

Research demonstrated that pretreatment of swine with α-tocopherol either in the diet or by injection stimulates the immune response so that resistance to infectious disease is improved (99). Polymorphonuclear neutrophils of cows injected with vitamin E and Se had a greater ability to kill phagocytized bacteria (45). Recent studies (152) gave evidence that an *agalactia toxemia* problem in sows postpartum could be ameliorated by supplementing the gestation and lactation diets with vitamin E and Se. Studies also demonstrated (67) the importance of vitamin E and Se in the dam's diet and consumption of colostrum for an adequate biological antioxidant status of the neonatal pig.

Recent studies demonstrated that there is an accumulation of riboflavin in uterine secretions of sows between days 6 and 8 of both the estrous cycle and of pregnancy (96). During this period, uterine flushings have a distinct yellow color, and total riboflavin in the flushings on day 8 of the estrous cycle was 134 μg. The importance of this high amount of riboflavin is not known but it occurs at the time of blastocyst development, which is a critical stage for embryonic survival. Gilts fed a riboflavin-deficient diet had progressively longer intervals between estrous periods and became anestrus after 63 days (36). Blood concentrations of progesterone and estradiol-17β were elevated in riboflavin-deficient gilts (36).

Zinc functions in the body as a component of many enzymes. Zinc was shown to be an important nutrient in swine in 1955 (138), several years before its importance in the human diet was recognized (114). The current recognition of the importance of zinc in T-cell function in immunocompetence began with our report of thymic atrophy in zinc-deficient pigs in 1968 (83). Recent studies (115) have shown beneficial effects of zinc supplementation of the diet of sickle-cell anemia patients, including improved growth, gonadal development, dark adaptation, and cell-mediated immunocompetence. There is a greatly lengthened parturition time in zinc-deficient sows (4.54 hr) compared to that of control sows (2.08 hr) (55). This effect of zinc deficiency is probably mediated through diminished gap junction formation, which has been observed in zinc-deficient pregnant rats. Zinc deficiency disrupts cell-to-cell communication and the timely establishment of estrogen dominance, and it impairs the transition steps necessary for the onset and completion of labor.

Copper deficiency in young growing pigs is manifest by microcytic hypochromic anemia, low ceruloplasmin levels, reduced erythrocyte life span, crooked legs with bone disorders, poor appetite, retarded growth, cardiac hypertrophy, aortic rupture, and ataxia (52, 103). In studies with high dietary zinc in gestation and lactation, we noted low plasma and tissue Cu in piglets (53). Normally, the fetal pig stores a reserve of Cu in the liver that after birth leaves the liver and enters the circulation. From a low value at birth plasma Cu levels increase seven-fold (27 to 195 μg/dl) within two weeks of birth (143). With the high level of Zn in the dam's diet, however, there is little fetal storage of Cu (53). We made use of this Zn-Cu interrelationship to provide a model for Cu deficiency in the baby pig and to establish the dietary Cu requirement of the baby pig at 5 ppm (52). The high Zn-to-Cu dietary ratio has also been shown to result in hypercholesterolemia (60). Providing supplemental Zn in the diet is effective in preventing neurologic symptoms observed in Wilson's disease patients (30). In this disease there is a defect in the biliary excretion of Cu. The Zn-Cu interaction effectively prevents the build up of excessive liver Cu levels.

Iron deficiency anemia in nursing baby pigs and nursing human babies is of universal concern (90) because milk is so low in iron (about 1 ppm). The baby pig has been an excellent model for studies because its iron deficiency develops very rapidly as a result of the tremendous relative growth rate of the nursing pig (1000% increase of birth weight in the first six weeks). The interaction of Cu and Fe is vital here because Cu as ceruloplasmin with its ferroxidase activity is vital in taking Fe from storage (ferritin and hemosiderin) and in allowing transferrin to pick up the Fe and transport it to the erythropoietic centers, where Fe is incorporated into protoporphyrin to make hemoglobin for the maturing reticulocyte.

Uteroferrin, an Fe-containing, progesterone-induced glycoprotein, is involved in maternal-to-fetal Fe transport in swine (31). Intramuscular injections of Fe dextran in sows on three occasions in early to mid pregnancy had a positive effect on Fe in allantoic fluid of the conceptus, uteroferrin in placentae, and neonatal hemoglobin values. This may provide a means of increasing fetal Fe stores to reduce problems of anemia in the piglet.

Iron is required by bacteria for growth and unless body Fe is bound by transferrin, uteroferrin, or lactoferrin, susceptibility to bacterial infection is enhanced. Oral or parenteral administration of Fe in amounts exceeding the minimum requirement to prevent anemia in nursing pigs should be avoided to minimize the amount of Fe not tightly bound (59, 62).

Soon after dietary Se was reported to prevent liver necrosis in rats (123), it was shown to be effective in preventing exudative diathesis in chicks (98), hepatosis dietetica in pigs (102), and white muscle disease in lambs (97). More recently, Se deficiency has been implicated as an etiologic factor in some forms of cancer (125) and cardiomyopathy of children in China, known as Keshan disease (57). Recognition of Se as an essential nutrient with established requirements for both pigs and people has been vital to their well-being.

CONCLUSION

It is apparent that there are important similarities and differences between pigs and people. Fortunately for those intent on studying digestive function, the morphology and physiology of the gastrointestinal systems are much alike. Both humans and pigs are highly dependent on dietary quality since symbiotic microorganisms within the gut play a relatively minor role in modifying the nutrients that are ingested. Ingesta transit times and digestive efficiencies are comparable. Postabsorptive metabolism is also similar in many respects, although the wide differences in length of gestation and the numbers of young born introduce a potentially significant divergence in nutrient needs for reproduction. Other interesting differences, such as the presence of carotenes in the plasma of humans that consume them and the absence of carotenes in the plasma of swine, should be recognized. Nevertheless, when minimum nutrient requirements of swine and established recommended daily allowances of humans are expressed per kilogram of dietary dry matter (assuming an intake of 500 to 800 g of dry matter per day by teenagers and adults), these values are highly related. It is only reasonable that one not draw unsupportable inferences from one species to another, but with the possible exception of nonhuman primates, it is apparent that the omnivorous pig is one of the best models for study of nutrition issues in the omnivorous human.

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