Amino Acid Nutrition for Optimum Growth, Development, Reproduction, and Health of Zoo Animals

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Abstract

Proteins are large polymers of amino acids (AAs) linked via peptide bonds, and major components for the growth and development of tissues in zoo animals (including mammals, birds, and fish). The proteinogenic AAs are alanine, arginine, aspartate, asparagine, cysteine, glutamate, glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine, and valine. Except for glycine, they are all present in the L-isoform. Some carnivores may also need taurine (a nonproteinogenic AA) in their diet. Adequate dietary intakes of AAs are necessary for the growth, development, reproduction, health and longevity of zoo animals. Extensive research has established dietary nutrient requirements for humans, domestic livestock and companion animals. However, this is not true for many exotic or endangered species found in zoos due to the obstacles that accompany working with these species. Information on diets and nutrient profiles of free-ranging animals is needed. Even with adequate dietary intake of crude protein, dietary AAs may still be unbalanced, which can lead to nutrition-related diseases and disorders commonly observed in captive zoo species, such as dilated cardiomyopathy, urolithiasis, gut dysbiosis, and hormonal imbalances. There are differences in AA metabolism among carnivores, herbivores and omnivores. It is imperative to consider these idiosyncrasies when formulating diets based on established nutritional requirements of domestic species. With optimal health, populations of zoo animals will have a vastly greater chance of thriving in captivity. For endangered species especially, maintaining stable captive populations is crucial for conservation. Thus, adequate provision of AAs in diets plays a crucial role in the management, sustainability and expansion of healthy zoo animals.

Keywords

Amino acids · Protein · Nutrition · Zoo animals · Captivity

Abbreviations

AA	amino acid
AAFCO	Association of American Feed Control Officials
BCAA	branched-chain amino acid
CP	crude protein
DM	dry matter
GABA	γ-aminobutyrate
NRC	National Research Council

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12.1 Introduction

Amino acids (AA) are nitrogenous, organic compounds consisting of both an amino group and an acid group (Wu 2018). All proteinogenic AAs have a carboxylic acid group, and non-proteinogenic AAs may contain a carboxylic acid [e.g., citrulline, ornithine, β-alanine, and γ-aminobutyrate (GABA)] or a sulfonic acid (e.g., taurine) group. Twenty proteinogenic AAs are precursors for protein synthesis (Wu et al. 2016), namely alanine, arginine, aspartate, asparagine, cysteine, glutamate, glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine, and valine. Some of them (e.g., glutamate, glycine and tryptophan) play an important role in chemical sensing in tissues [including the skin and digestive tract (Solano 2020; Wu 2020c)], as well as in intestinal and pulmonary immune and antioxidative responses (Beaumont and Blachier 2020; Chen et al. 2020; Ren et al. 2020). Although non-proteinogenic AAs are not required for protein synthesis, they (e.g., taurine and GABA) have important physiological functions and their deficiencies can result in multi-organ abnormalities (Bazer et al. 2015; Wu 2020a, b). Furthermore, some end products of AA metabolism, such as felinine, isovalthine, and isobuteine (Fig. 12.1) produced by certain members of the Felidae species, may serve as territorial marks and intra-species communication signals in animals (Che et al. 2020; Miyazaki et al. 2008).

Protein or AA requirements for zoo animals (Allen and Ullrey 2004), like livestock and poultry (Wu 2018), vary among different stages of their growth and development and in response to alterations in nutritional, environmental, and pathological conditions. For example, the mink (a carnivore) is not able to synthesize arginine de novo (NRC 1982), whereas tigers and cheetahs (carnivores) do not produce taurine just like domestic cats (Gelatt 2014). In addition, mammals (Hou and Wu 2018) and birds (Wu 2009), as well as carnivorous and omnivorous fish (Jia et al. 2017; Li et al. 2020a) need large amounts of glutamate and glutamine for the growth and health of their small intestine. Much work has been done in recent years to establish optimal AA requirements for domestic livestock species, birds, fish, and humans (Wu 2009, 2018). Traditionally, AAs have been classified as nutritionally essential (EAA) or non-essential (NEAA; Wu 2010). The carbon skeletons of EAAs cannot be synthesized *de novo* by the body or cannot be synthesized in an adequate amount; therefore, these AA must be provided in diets (Wu 2009). Even though the body is able to synthesize NEAAs, their formation may not be adequate for maximal growth and optimal health, especially at certain physiological stages, such as pregnancy, lactation, and growth after weaning

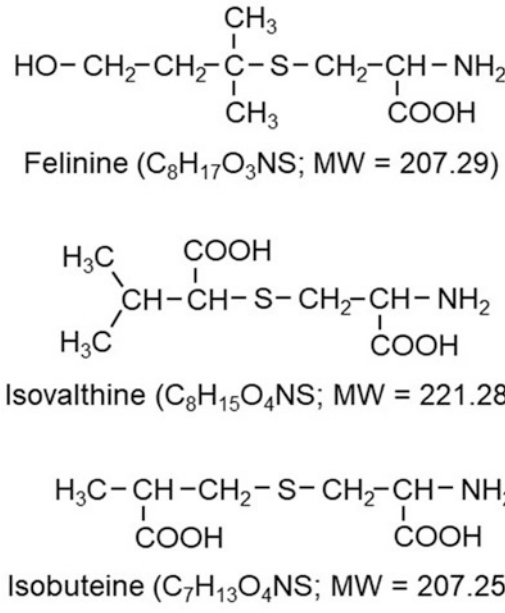

Fig. 12.1 Chemical structures of felinine (2-amino-7-hydroxy-5,5-dimethyl-4-thiaheptanoic acid; (2*R*)-2-amino-3-[(3-hydroxy-1,1-dimethylpropyl)thio]propanoic acid]), isovalthine (2-amino-5-carboxy-6-methyl-4-thiaheptanoic acid), and isobuteine [2-amino-6-carboxy-4-thiaheptanoic acid; *S*-carboxyisopropylcysteine; *S*-(2-methyl-2-carboxyethyl)cysteine]. Certain members of the Felidae family (e.g., cats) synthesize and excrete these three unique sulfur-containing amino acids.
In addition, humans with hypothyroidism and hypercholesterolemia, as well as other select mammals (e.g., the rat, rabbit, guinea pig, and dog) are known to produce isovalthine

(Hou and Wu 2017; Hou et al. 2015; Wu et al. 2017, 2018). For this reason, dietary requirements of zoo animals for NEAAs must be established.

For zoo and endangered animals, it is difficult to determine exact dietary nutritional requirements due to the invasive nature of the methods used (Schmidt et al. 2007). Therefore, domestic animals are often employed to estimate dietary nutritional requirements for captive carnivores, herbivores, and omnivores (Schmidt et al. 2007). However, these estimations may not be completely accurate considering unique biochemical and physiological differences among species. Even when analyzing nutrient concentrations in the serum of a captive exotic animal is possible, the results may be vastly different from those in a free-ranging animal because differences in nutrient intakes [e.g., dry matter (DM), AAs, carbohydrates, vitamins, and minerals] and blood hormone levels (Schmidt et al. 2007).

The major objective of this article is to highlight unique features of AA nutrition and metabolism in zoo animal species based on the limited data available. Due to the complicated processes necessary to define nutritional requirements of zoo animals, it is important to use the information established for domestic species (e.g., sheep, cattle, pigs, chickens, and farmed fish) and make adjustments based on observations to best formulate adequate diets for zoo animals.

12.2 Carnivores

Carnivores, by definition, eat animals or animal products and have unique physiological features that support the consumption and digestion of prey. Their diets are rich in protein and fats, but contain a very small amount of carbohydrate. Thus, carnivores must synthesize a large amount of glucose from AAs (Ala, Arg, Asp, Asn, Cys, Gln, Glu, Gly, His, Met, Pro, Ser, Thr, and Val that can produce pyruvate and an intermediate of the Krebs cycle) in the liver and kidneys to support the metabolic needs of their brain, red blood cells, retina, and kidney medulla (Wu 2018). Based on studies with cats and dolphins, carnivores lack hepatic glucokinase (for glycolysis and glucose sensing) and hepatic glucokinase regulatory protein, and are prone to periods of fasting hyperglycemia, contrary to monogastric mammals (Schermerhorn 2013). This class of animals includes mammal obligate carnivores [i.e. felids (e.g., domestic cats, tigers, and lions), giant anteaters, otters, hyenas, sea lions, mink, tarsiers, dolphins, seals, and walruses] and non-mammal obligate carnivores (e.g., largemouth bass, rainbow trout, salmon, hawks, eagles, crocodilians, many snakes and lizards, and most amphibians]. Obligate carnivores must eat animals or animal products because they lack the enzymes to synthesize or metabolize certain nutrients that cannot be obtained from plants and bacteria (Kleiman et al. 2010). As an example, felids do not synthesize either ornithine, citrulline and arginine from glutamic acid or taurine from cysteine (MacDonald et al. 1984).

Ornithine serves as an intermediate for urea synthesis in mammals by stimulating the conversion of ammonia, a product of protein metabolism, into urea for excretion (Wu 2013). Ornithine can also be used for proline synthesis or converted into polyamines (putrescine, spermidine and spermine), which are important regulators of DNA and protein synthesis (Wu 2013). As an allosteric activator of *N*-acetylglutamate synthase, arginine is also a crucial AA for urea-cycle function and ammonia detoxification as urea in mammals (Wu and Morris 1998). Thus, cats (which cannot synthesize arginine due to an intestinal deficiency of pyrroline-5-carboxylate synthase) develop severe hyperammonemia after consuming an arginine-free diet, which often quickly leads to death (Baker 2007). Severe hyperammonemia occurs in cats since they cannot synthesize ornithine, and therefore citrulline, which limits renal arginine synthesis (Ball et al. 2007). As obligate carnivores, cats eat high levels of protein, and therefore, need high levels of dietary arginine for urea-cycle function and nitrogen excretion. Likewise, mink grow very poorly and die when fed an arginine-free or deficient diet (NRC 1982).

Taurine is critical for regulating intracellular osmolality and retinal photoreceptor activity, modulating the digestion and absorption of dietary fats and lipid-soluble vitamins, as well as the nervous, muscular and reproductive systems, and

it is also a major antioxidant (Wu 2018). As in domestic cats (Che et al. 2020), the concentrations of taurine in the plasma and whole blood of zoo felids [the fishing cat (*Prionailurus viverrinus*), lion (*Panthera leo*), Bengal tiger (*Panthera tigris tigris*), Siberian tiger (*Panthera tigris altaicia*); cheetah, leopard (*P. pardus*), cougar (*Puma concolor*), and serval (*Leptailurus serval*)] are 80–120 and 300–600 nmol/ml, respectively (Hedberg et al. 2007). The ability of carnivores to synthesize taurine varies greatly among species and even the different breeds of the same species. For example, unlike domestic cats, tigers, lions and other felids (e.g., the cheetah, puma, jaguar, and leopard; Chesney and Hedberg 2009; Gelatt 2014), most of dog species are able to synthesize taurine from cysteine in the liver (Hayes 1998). However, certain breeds of dogs [e.g., giant breed dogs (Newfoundland) and American Cocker Spaniels] and some individuals do not synthesize taurine due to genetic defects and must require a dietary source of taurine to maintain health and prevent disorders, such as dilated cardiomyopathy and retinal lesions (Backus et al. 2003; Fascetti et al. 2003; Kittleson et al. 1997). Anderson et al. (1979) found that 0.1% taurine in the diet supports sufficient growth in kittens and prevents tissue depletion of taurine. However, with a taurine-free diet, photoreceptor degeneration occurs in the retina due to taurine depletion, while glycine and glutamine concentrations increase in the area centralis of the retina and in the heart (Anderson et al. 1979). Concentrations of glutamine also increase in the lens of the eye, which alters the glutamine: glutamate ratio (Anderson et al. 1979). Cats and dogs use solely taurine to conjugate bile acids via *N*-acylamidation, but other species use both glycine and taurine to do so (Czuba and Vessey 1981). Bile acid conjugation plays an important role in the digestion and absorption of dietary lipids, as well as liver physiology and the intestinal microflora (Hagey et al. 2010; Wu 2018). At present, little is known about bile acid-conjugating enzymes in zoo animals, including carnivores. However, studies with 677 vertebrate species (103 fish, 130 reptiles, 271 birds, 173 mammals) have shown significant variation in bile salt composition among orders but not between families, genera, or species (Hofmann et al. 2010).

Some Felidae species (e.g., the bobcat, ocelot, Chinese desert cat, kodkod, Siberian lynx, and domestic cat) have been reported to synthesize felinine (2-amino-7-hydroxy-5,5-dimethyl-4-thiaheptanoic acid; (2*R*)-2-amino-3-[(3-hydroxy-1,1-dimethylpropyl)thio]propanoic acid]) (Hendriks et al. 1995; Miyazaki et al. 2008; Westall 1953). In addition, certain felids (e.g., the domestic cat and the lion), as well as humans with hypothyroidism and hypercholesterolemia and other select mammals (e.g., the rat, rabbit, guinea pig, and dog) are known to produce isovalthine (2-amino-5-carboxy-6-methyl-4-thiaheptanoic acid) (Kuwaki et al. 1963; Mizuhara and Oomori 1961). Furthermore, the domestic cat, other select members of the Felidae family, and humans generate isobuteine [2-amino-6-carboxy-4-thiaheptanoic acid; *S*-carboxyisopropylcysteine; *S*-(2-methyl-2-carboxyethyl)cysteine] (Kodama et al. 1980; Oomori and Mizuhara 1962).

Felinine, isovalthine, and isobuteine are unusual sulfur-containing AAs in that they contain both a sulfur atom in the main chain and a branched side chain with a methyl group. Their syntheses require glutathione and either an isoprene unit or a branched-chain α-ketoacid, as illustrated for feline in Fig. 12.2. Specifically, in the livers of those species, glutathione conjugates with isopentenyl pyrophosphate [an intermediate of cholesterol biosynthesis (Rutherfurd et al. 2002)], isovaleric acid [a metabolite of leucine (Rutherfurd-Markwick et al. 2005)], and possibly isobutyric acid (a metabolite of valine) to yield 3-methylbutanol-glutathione (3-mercaptobutanol-glutathionine; γ-glutamylfelinylglycine), *S*-(iso-propylcarboxymethyl)-glutathione, and *S*-(iso-ethylcarboxymethyl)-glutathione, respectively. These conjugation reactions are catalyzed by glutathione *S*-transferase in the cytosol of hepatocytes. The glutathione conjugates are released from the liver and transported in the blood to the kidneys, where they are metabolized via γ-glutamyl transferase (a membrane-bound

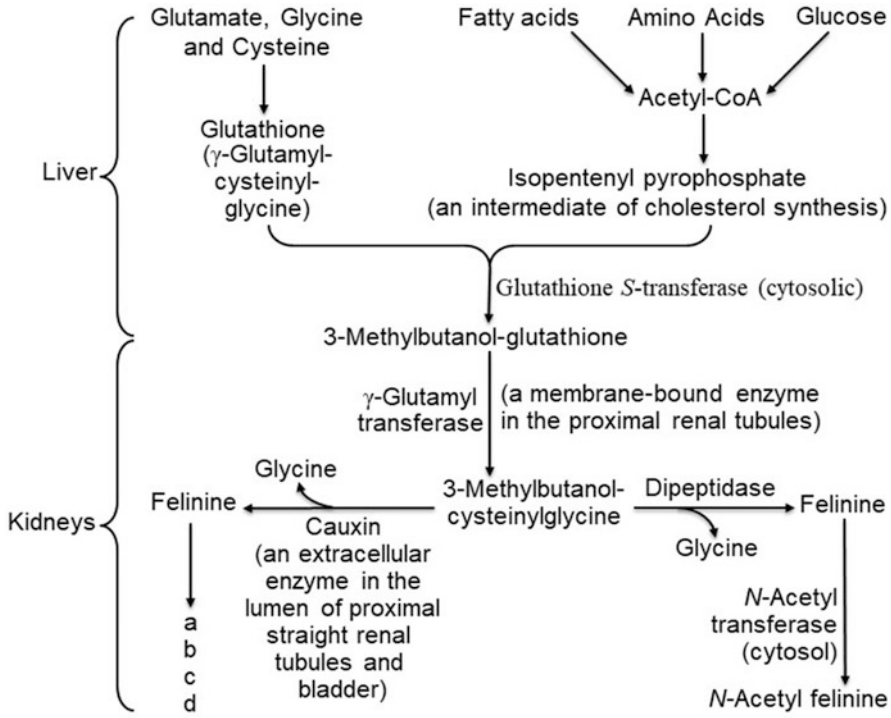

Fig. 12.2 Synthesis and metabolism of felinine in domestic cats. In the liver of domestic cats, glutathione *S*-transferase catalyzes the conjugation of glutathione with isopentenyl pyrophosphate yield 3-methylbutanol-glutathione. The latter is released from the liver and transported in the blood to the kidneys, where it is metabolized via γ-glutamyl transferase (a membrane-bound enzyme in the proximal renal tubules) to form 3-methylbutanol-cysteinylglycine. This cysteinylglycine derivatives is hydrolyzed by dipeptidases (e.g., aminopeptidase M) in the cytosol of the proximal renal tubules to generate felinine, with glycine as a co-product. Felinine is locally *N*-acetylated by *N*-acetyltransferase to *N*-acetyl-felinine. Additionally, 3-methylbutanol-cysteinylglycine is hydrolyzed by the extracellular cauxin (a carboxylesterase secreted by the proximal straight renal tubules of the kidneys) in the lumen of the renal tubules and the bladder to yield felinine, with glycine as a co-product. In the cytosol of the proximal straight renal tubules, feline is further metabolized into methylated products (a, b, c and d). a = 3-mercapto-3-methyl-1-butanol; b = 3-mercapto-3-methylbutyl formate; c = 3-methyl-3-methylthio-1-butanol; and d = 3-methyl-3-(2-methyldisulfanyl)-1-butanol. Felinine and its derivatives are excreted in the urine

enzyme in the proximal renal tubules) to form 3-methylbutanol-cysteinylglycine, *S*-(iso-propylcarboxymethyl-cysteinylglycine, and *S*-(iso-ethylcarboxymethyl-cysteinylglycine, respectively. These cysteinylglycine derivatives are hydrolyzed by dipeptidases (e.g., aminopeptidase M) in the cytosol of the proximal renal tubules to generate felinine, isovalthine, and isobuteine, respectively, with glycine as a co-product.

Some of the resultant sulfur-containing metabolites are locally *N*-acetylated by *N*-acetyltransferase to their corresponding acetyl derivatives (i.e., *N*-acetyl-felinine, *N*-acetyl-isovathine, and *N*-acetyl-isobuteine, respectively). Additionally, 3-methylbutanol-cysteinylglycine, *S*-(iso-propylcarboxymethyl-cysteinylglycine, and*S*-(iso-ethylcarboxymethyl-cysteinylglycine are hydrolyzed by the extracellular cauxin (a carboxylesterase secreted by the proximal straight renal tubules of the kidneys) in the lumen of the renal tubules and the bladder to yield felinine, isovalthine, and isobuteine, respectively, with glycine as a co-product. In the cytosol of the proximal straight renal tubules, feline is further metabolized into 3-mercapto-3-methyl-1-butanol, 3-mercapto-3-methylbutyl formate, 3-methyl-3-methylthio-1-butanol, and 3-methyl-3-(2-methyldisulfanyl)-1-butanol (Miyazaki et al. 2008). Similar modifications of isovalthine, and isobuteine may also occur. Felinine,

isovalthine, and isobuteine, as well as their derivatives are excreted in the urine.

The syntheses of felinine, isovalthine, and isobuteine are influenced by dietary intakes of methionine and cysteine (Hendriks et al. 2008; Rutherfurd-Markwick et al. 2005), and possibly dietary lipids (in the case of felinine), leucine (in the case of isovalthine), and valine (in the case of isobuteine) when the dietary provision of methionine, cysteine, glycine, and BCAAs is not limiting. Interestingly, the production of felinine by felids is gender-specific as its excretion in the urine is much higher in males than in females (Rutherfurd-Markwick et al. 2005), but the urinary excretion of isovalthine by adult cats is not gender-specific (Hendriks et al. 2004).

The biological significance of felinine, isovalthine, and isobuteine, as well as their derivatives remains largely elusive. It is possible that these sulfur-containing AA and their metabolites serve as non-toxic, non-reactive, and relatively stable end products of Met and Cys to prevent excessive formation of toxic and highly acidic substances (e.g., H_2S, SO_2, and H_2SO_4) from Met and Cys. Of particular note, Miyazaki et al. (2008) have suggested that felinine is a territorial marker for intra-species communications and is also a putative precursor of a pheromone that serves as a chemical signal to attract females. This explains, in part, an important role of dietary AAs in the physiology and behavior of zoo animals of either the same or different species.

Either inadequate nutrition (especially deficiencies in certain AAs) or excessive AAs lead to nutrition-related diseases and disorders (Oberbauer and Larsen 2020; Wu 2020a). Urolithiasis (the process of forming stones in the kidenys, bladder and/or urethra) occurs when mineral crystals precipitate from the urine and form uroliths in the urinary tract (Kleiman et al. 2010). There are different types of uroliths that may form from different nutrients and minerals in the diet. In canids, a high-protein diet may cause ammonium urate stones or cystine uroliths (Kleiman et al. 2010). Cystine has a poor solubility at physiological pH and in acidic urine, and may lead to cystine uroliths in dogs that have a defect in reabsorption of cystine and other basic AAs in the kidneys (Kleiman et al. 2010). As previously stated, felids are strict carnivores and require taurine in the diet, but canids, bears, and giant anteaters also have a dietary requirement for taurine (Kleiman et al. 2010). Dilated cardiomyopathy, bilaterally symmetrical hyper-reflective retinal lesions, poor reproduction, and progressive exercise intolerance and dyspnea have all been associated with a taurine deficiency in those animals (NRC 2006). These nutrition-related diseases highlight the importance of balanced diets with adequate AA composition in addition to the optimal overall protein content.

The giant anteater (*Mymercophaga tridactyla*) is an insectivore, a specific type of carnivore, which also commonly experiences side effects of taurine deficiency, such as dilated cardiomyopathy, in captivity (Nofs et al. 2018). Exact nutrient requirements for the giant anteater have not been established, but analyses of some diets revealed taurine levels between 0.11 and 0.18 g/kg DM (Nofs et al. 2018). As a comparison, the recommended taurine level for dry food for cats, another carnivore, is 1.0 g/kg DM (AAFCO 2012). Assuming that taurine homeostasis in giant anteaters is regulated by urinary excretion of taurine and that urinary taurine concentration varies directly with body taurine status, Nofs et al. (2018) analyzed urinary taurine concentrations in response to taurine and methionine supplementation to a commercially available insectivore diet. It was found that urinary taurine excretion increased with increasing dietary taurine intake and also increased with methionine supplementation, indicating that giant anteaters can synthesize adequate amounts of taurine from methionine (Nofs et al. 2018). Figure 12.3 illustrates how methionine is metabolized to homocysteine, which is further converted to cysteine by cystathionine γ-lyase; cysteine is then converted into taurine (Fig. 12.3). These findings suggest that giant anteaters can synthesize adequate

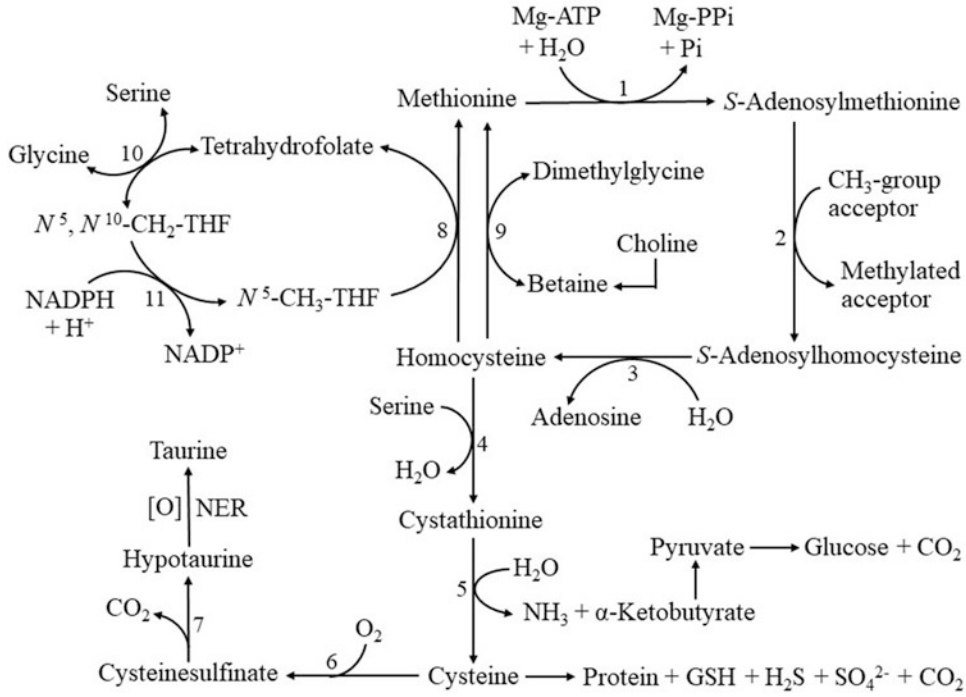

Fig. 12.3 Synthesis of taurine from sulfur-containing amino acids (methionine and cysteine) in animals. The enzymes catalyzing the indicated reactions are: (1) *S*-adenosylmethionine synthase; (2) methylase; (3) *S*-adenosylhomocysteinase; (4) cystathionine β-synthase; (5) cystathionine γ-lyase; (6) cysteine dioxygenase; (7) cysteinesulfinate decarboxylase; (8) methionine synthase; (9) betaine:homocysteine methyltransferase; (10) serine hydroxymethyltransferase; (11) N^5-N^{10}-methylene- tetrahydrofolate reductase; GSH = glutathione; α-KB = α-ketobutyrate; NER = nonenzyme catalyzed reaction; N^5, N^{10}-CH_2-THF = N^5, N^{10}-methylene tetrahydrofolate; N^5-CH_3-THF = N^5-methyl-tetrahydrofolate

amounts of taurine as long as the diet contains sufficient amounts of methionine or cysteine (Nofs et al. 2018).

For carnivorous species in zoos, whole prey items are commonly used as a dietary source, as well as enrichment to mimic species-typical behavior (Kerr et al. 2014). However, these whole prey diets tend to exceed the protein requirements established by the NRC (2006) for dogs and cats or livestock species and do not focus on specific AA requirements. Dierenfeld et al. (2011) found that all the domestic meats tested were limiting in arginine, leucine, methionine + cystine, and phenylalanine + tyrosine compared to the requirements for obligate carnivores. However, this is not true for beef (Wu et al. 2016) and some animal-source feedstuffs (Li and Wu 2020). Generally, lysine is considered as the first limiting AA when calculating ideal protein ratios, but these ratios are species-specific (Dierenfeld et al. 2011). The cecectomized rooster assay was determined to be an appropriate model for evaluating AA digestibility of animal products that may be fed as whole prey to captive exotic felids to validate that these food sources are meeting the nutritional requirements (Kerr et al. 2014). Compared to The Association of American Feed Control Officials (AAFCO 2012) recommendations for domestic cats, ground duck had a slightly lower combined concentration of methionine + cysteine than that recommended for growth, reproduction, and adult maintenance (Kerr et al. 2014). Because some methionine and cysteine in feedstuffs are oxidized under acid hydrolysis conditions at 110 °C, caution should be taken to ensure that the content of these two sulfur-containing AAs in protein is analyzed properly (Dai et al. 2014). For ground duck,

150 to 180 day-old mice, 30- to 45-day -old rabbits, and rabbits more than 65 days of age, concentrations of taurine in their blood were lower than values recommended by AAFCO (2012) and Kerr et al. (2014).

Protein quality and concentration can also have an effect on the microbiota in the gut of carnivores (Madsen et al. 2017). Even though carnivores do not rely heavily on microbial fermentation in the gut for energy, the microbiota population has an effect on gastrointestinal and whole body functions, such as digestion, inflammation, and pathogen resistance (Lubbs et al. 2009; Wasimuddin et al. 2017). Captive animal populations tend to have less diversity in their microbome compared to their free-ranging counterparts due to differences in their diet (Wasimuddin et al. 2017). According to Wasimuddin et al. (2017), captive cheetahs have a higher prevalence of potential pathogenic bacteria than free-ranging cheetahs when analyzing fecal samples with 16S rRNA gene high-throughput sequencing. Lower quality protein may not be adequately digested in the small intestine, which allows more AAs in dietary protein to enter the large intestine and increases the activity of its proteolytic bacteria (Amstberg et al. 1980; Lubbs et al. 2009). Also, more protein in the lower bowel may result in increased production of ammonia, sulfur-containing compounds, indoles, and phenols, all of which become toxic at high concentrations in the body (Lubbs et al. 2009). In domestic cats fed a high-protein diet, there was a shift from carbohydrate-fermenting bacteria to proteolytic bacteria, which may be pathogenic (i.e. *Clostridium*) (Lubbs et al. 2009). Similarly, Cheetahs in captivity experience a high prevalence of *Heliobacter* infections, leading to chronic gastritis (Wasimuddin et al. 2017), and both lions and cheetahs are known to suffer from *Clostridium sordelli* and *Clostridium perfringens* (de la Fe et al. 2006). Captive marine carnivores, such as the Australian sea lion, also experience changes in the gut microbiota, compared to wild sea lions due to less diverse protein sources (Delport et al. 2016). Reducing total protein content and balancing all proteinogenic AAs in the current commercial diets may be beneficial for improving intestinal health in carnivores.

12.3 Herbivores

Herbivores eat predominantly plant matter and have symbiotic microorganisms in the gut that help to digest plant matter by anaerobic fermentation to supply the animal with energy (Wu 2018). Herbivores can be divided into two different subgroups: pregastric fermenters and postgastric fermenters. Ruminants are pregastric fermenters and have a compartmentalized stomach containing a rumen where microbial fermentation occurs (i.e. cattle, sheep, deer, giraffe, kangaroos, and antelope; Kleiman et al. 2010). By definition, ruminants regurgitate their food to remasticate, resalivate and reswallow for further digestion (Kleimen et al. 2010). In contrast to carnivores, ruminants do not have a high dietary requirement for AAs and vitamins because the microorganisms of the rumen have the ability to synthesize protein from non-protein and non-AA nitrogen such as urea and ammonia (Kleiman et al. 2010; Wu 2013). Nonruminant pregastric fermenters also have a compartmentalized stomach for microbial fermentation, but do not regurgitate their food for further digestion (i.e. hippopotamuses, kangaroos, and langur primates; Kleiman et al. 2010). Postgastric herbivores have a large cecum and colon where microbial fermentation occurs (i.e. horses, capybaras, rabbits, rhinoceroses, elephants, and apes; Kleiman et al. 2010). The growth, development, health, and survival of herbivores (including ruminants) depend on the unique characteristics of their digestive systems (Wu 2005). All herbivores are able to synthesize taurine from cysteine in their liver, but the rates of the synthesis of taurine vary among animal species (Hou et al. 2020; Jacobsen and Smith 1968; Sturman and Hayes 1980; Wright et al. 1986).

Nutrient requirements of zoo animals are based on similar domestic species with established nutrient requirements; however, these are not always accurate comparisons. Serum concentrations of AAs in free-ranging giraffes from two game

reserves in South Africa were compared with serum concentrations of AAs in steers and sheep which showed apparent differences in concentrations of cystine, isoleucine, and valine (Schmidt et al. 2007). The concentrations of free cystine in free-ranging giraffes from Double Drift Game Reserve and Kariega Game Reserve were 0.19 mg/dL (7.9 μM) and 0.35 mg/dL (14.6 μM), respectively, compared to 4.52 mg/dL (188 μM) in sheep (Schmidt et al. 2007). The concentrations of free cystine in the serum of zoo giraffes (United States) fed an alfalfa-based diet and free-ranging giraffes (South Africa) were 0.00 mg/dL (0.0 μM) and 0.22 mg/dL (9.2 μM), respectively (Schmidt et al. 2009). The concentration of free cysteine in the serum of captive sheep is similar to the concentration of total free cysteine (cysteine + ½ cysteine; 188 μM) in the plasma of adult sheep fed an alfalfa-based diet (Kwon et al. 2003). However, the reported concentrations of cystine (the major oxidized dimer form of cysteine in animals; 0.0 to 15 μM) in the serum of adult giraffes are too low to be compatible with life and may not represent its true values, but rather might be due to problems with its analysis because the determination of this AA is a technical challenge (Wu 2013). This underscores the importance of accurate analyses of AAs in studying the protein and AA nutrition of animals.

Similar to carnivores, herbivores can also experience urolithiasis, the precipitation and formation of mineral crystals from the urine in the urinary tract (Kleiman et al. 2010). Sheep may have a high cysteine requirement for wool production, but Schmidt et al. (2007) has shown that concentrations of cysteine in the serum of giraffes are significantly reduced when compared to those for sheep, suggesting that the use of the data on dietary nutrient requirements of sheep to establish dietary nutrient requirements for giraffes may not be fully justified. Further studies are warranted to validate these intriguing findings before recommendations for changes in the diets of zoo giraffes are recommended. In blood, most (97%) cysteine is spontaneously oxidized to cystine (Wu et al. 1997). Among all physiological AAs, cysteine has the lowest solubility (0.46 mM) in water at 25 °C and neutral pH (Wu 2013). Thus, high concentrations of cystine in the diet could contribute to the prevalence of urolithiasis in captive giraffes.

Isoleucine concentrations in the serum of giraffes were 2.07 and 2.01 mg/dL from the two game reserves compared to 0.79 and 0.87 mg/dL in steers and sheep, respectively (Schmidt et al. 2007). Concentrations of valine in serum of giraffes from the two game reserves were 4.64 and 4.60 mg/dL, compared to 1.53 and 2.00 mg/dL in steers and sheep, respectively (Schmidt et al. 2007). Isoleucine and valine are branched-chain amino acids (BCAAs) along with leucine, and all the three BCAAs must be balanced to gain advantage of their physiological functions (Wu 2009). For example, BCAAs are important for protein synthesis by activating the mechanistic target of rapamycin cell-signaling pathway (Wu 2009; Zhang et al. 2019). Skeletal muscle can synthesize glutamine and alanine from BCAAs and glucose (the primary precursor of α-ketoglutartae and pyruvate). Glutamine has a variety of metabolic functions including gluconeogenesis, cell proliferation, synthesis of NAD(P), regulation of protein turnover, and synthesis of purine, pyrimidine, ornithine, citrulline, arginine, proline, and asparagine (Wu 2009). A balance of dietary BCAAs is crucial for optimal health of all animals to prevent antagonisms among the AAs. However, dietary requirements of giraffes for the BCAAs and other AAs should not be based solely on their concentrations in the serum or plasma of giraffes or other ruminant species (such as cattle and sheep), because the circulating levels of AAs are influenced by many factors (e.g., physiological, pathological, and environmental) other than diets and because there are significant differences in concentrations of AAs in serum among animal species (Wu 2018).

Caution should be exercised when feeding zoo animals a diet similar to that for their domesticated counterpart so as to prevent disruption of the gut microbiome. As previously stated, the microbial population of the gut in herbivores is essential for the digestion of fiber and production of short chain fatty acids and AAs. Gibson et al. (2019) found a significant difference in diversity of the gut microbiome in captive black rhinoceroses, compared to wild black rhinoceroses. The captive rhinos showed an increase in glycolysis and AA syntheses in the

microbial populations, suggesting an imbalance of nutrients in their diets (Gibson et al. 2019).

12.4 Omnivores

Omnivores are animals that consume both plant and animal matter (i.e. pigs, bears, foxes, raccoons, many primates, giant pandas, maned wolves, and some canids). Because the composition of AAs differ between plant- and animal-source feedstuffs (Hou et al. 2019; Li and Wu 2020), dietary intakes of many AAs (particularly methionine, cysteine, glycine, proline, and tryptophan) by these animals critically depend on their food sources. The digestive physiology of omnivores allows the consumption and digestion of meat and plant material, but the intestines of these animals except for certain species (e.g., grizzly bears, black bears, and giant pandas) have a limited capacity for the microbial fermentation of plant fibrous material in the gastrointestinal tract (Kleiman et al. 2010; Pritchard and Robbins 1990). Unlike carnivores, omnivores do not have a strict requirement for meat but rather base their diets on seasonally available feedstuffs in their habitat (Kleiman et al. 2010). Most omnivores are able to synthesize taurine from cysteine in their livers, with the rates of synthesis depending on species (Jacobsen and Smith 1968; Sturman and Hayes 1980; Wright et al. 1986). It is important to consider the ratio of plant- and animal-source feedstuffs in the natural diet of omnivores because over- or under-feeding of macro and micronutrients may result in nutrition-related diseases. Maned wolves tend to eat a higher proportion of plant material than other species of wolves that consume primarily meat (Kleiman et al. 2010). In U.S. zoos, maned wolves are fed diets primarily consisting of red meat, which has high concentrations of sulfur-containing AAs, leading to a decrease in urinary pH and the formation of cystine uroliths that can also occur in some herbivores and carnivores (Phipps and Edwards 2009; Kahn and Line 2005). However, protein-restrictive diets result in taurine deficiency and fecal inconsistency in maned wolves (Sanderson et al. 2001), suggesting that this animal species may have little or no ability to synthesize taurine. Canids that develop cystinuria also have an increased chance of developing a carnitine deficiency (Sanderson et al. 2001). Like cystine, carnitine is reabsorbed by the renal glomerulus into the blood circulation via a sodium-dependent transport system (Wu 2018). Carnitine is derived from methionine and lysine, and required for the transport of long chain fatty acids from the cytosol into mitochondria for oxidation and ATP production (Wu 2018). Because of these issues, much research is needed to formulate a specific diet for captive maned wolves for optimal health.

Bears are considered omnivores and have the digestive physiology of carnivores (e.g., having a single stomach and a short intestine), whereas giant pandas (also known as the panda bear) with the digestive system of carnivores live as herbivores consuming almost exclusively bamboo. Giant pandas do not rely primarily on microbial fermentation of plant fibrous material to meet their nutrient requirements, but are able to survive by eating a large amount of bamboo (e.g., up to 6% of body weight in DM per day by a 120-kg adult) despite their inefficient digestive system for utilizing plant fibrous material (Dierenfeld et al. 1982; Schaller et al. 1985). Bamboo contains 8.6% CP, 74.6% cell wall material (including 29.7% hemi-cellulose, 26.5% cellulose, and 7.3% lignin), and 4.8 kcal/g gross energy (all on the DM basis; Dierenfeld et al. 1982). For comparison, an adult steer (540 kg) consumes DM at 2.6% of body weight per day (Gilbreath et al. 2020). Interestingly, the passage of digesta through the gastrointestinal tract of the giant panda is very rapid (< 12 h), and the digestibility coefficients of bamboo DM (largely crude fiber), hemicellulose, and cellulose in adult giant pandas are 20%, 27%, and 8%, respectively (Dierenfeld et al. 1982). Cellular contents (AAs, protein, sugars, and starch) are the main sources of nutrients for giant pandas.

The gut microbiome of giant pandas closely resembles the gut microbiome of a carnivore with a high abundance of genes encoding for enzymes for AA degradation and a low abundance of genes for enzymes related to cellulose- and

hemicellulose-digestion (Guo et al. 2018; Xue et al. 2015). Specifically, despite its ability to metabolize dietary cellulose (Zhu et al. 2011), the gut microbiota of giant pandas is abundant in *Escherichia, Shigella* and *Streptococcus* bacteria that are normally found in carnivores for protein digestion (Xue et al. 2015) and in genes that are associated with the degradation of glutamine and glutamate (glutaminase, glutamate decarboxylase, GABA-transaminase, and succinic semialdehyde dehydrogenase; Fig. 12.4), similar to carnivores and other bears (Guo et al. 2018). Thus, we surmise that there is active nitrogen metabolism and recycling in the intestine of giant pandas for AA utilization, as reported for such omnivores as humans, pigs, rats and ruminants (Bergen and Wu 2009). This, however, may not be able to fully compensate for the low AA content of bamboo and its low digestibility (Dierenfeld et al. 1982), such that giant pandas may not have adequate protein nutrition for optimum growth, gestation and lactation. In support of the suggestion, the female giant panda ovulates only once a year in the Spring season, and implantation of her fertilized egg is delayed for 2 to 3 months until the leaves and shoots of bamboo become more abundant and contain more nutrients (e.g., AAs and calcium) to support embryonic growth and development (Schaller et al. 1985; Zhang et al. 2018). Despite the reproductive and foraging strategies of gestating giant pandas, as well as a gestation length of 96 to 158 days between insemination and parturition (Zhang et al. 2009), the average birth weight of their offspring (almost 50% singletons and 50% twins) is only 90–130 g (Schaller et al. 1985). For comparison, in domestic pigs, which usually gestate 10 to 14 live fetuses, average fetal weights on days 60, 90, and 114 (term) of gestation are 130, 596, and 1486 g, respectively (Wu et al. 2013). Improving the supply of AAs (particularly arginine and glutamine) may enhance fetal survival and growth in giant pandas, as reported for swine (Wu et al. 2010, 2011).

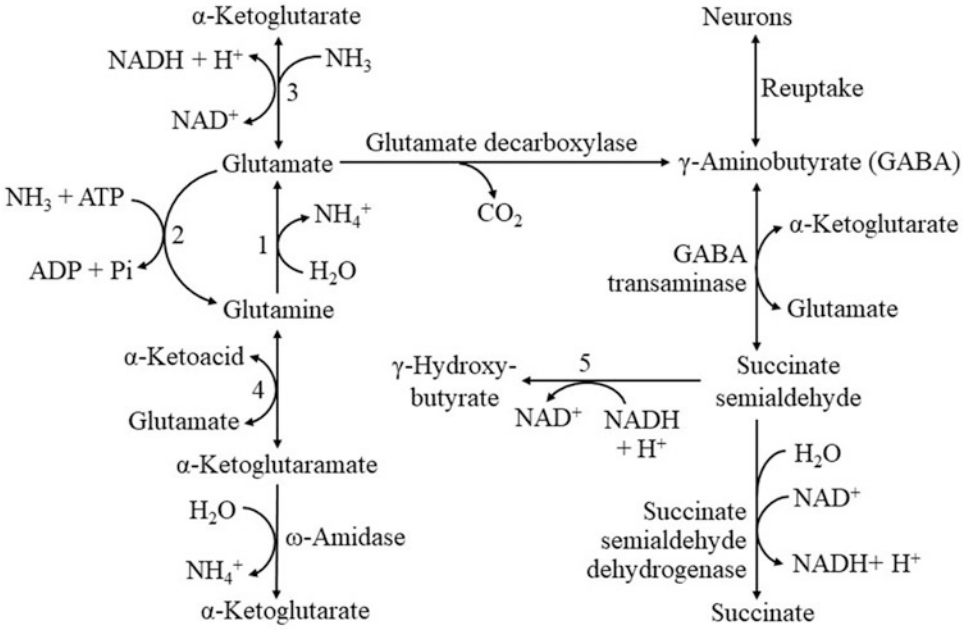

Fig. 12.4 Catabolism of glutamine and glutamate in zoo animals. The enzymes in these specific pathways of glutamine and glutamate metabolism are up-regulated in pandas, as well as other bears and carnivores. In comparison, herbivores have greater expression of enzymes associated with the synthesis of glutamine and glutamate (i.e. glutamine synthetase, glutamate synthase, and glutamate dehydrogenase). The enzymes catalyzing the reactions are: (1) phosphate activated glutaminase; (2) glutamine synthetase; (3) glutamate dehydrogenase; (4) glutamine transaminase; and (5) succinate semialdehyde reductase

The nutrient requirements for most subhuman primates are based on dietary nutrient requirements of humans. The CP of normal diets of captive apes, lemurs and marmosets provides between 9.5% and 13% of the energy intake, compared to the normal 10% to 12% in humans (King 1978). However, nutrient requirements of primates are only based on a few species of primates and specific needs may vary among species; and protein requirements seem to be different for New World primates, compared to Old World primates (Crissey and Pribyl 2000). The protein requirement of New World primates may be closer to 25% of the diet, but the NRC (1978) has established the minimum protein requirement of primates to be 16% for all stages of life (Crissey and Pribyl 2000). Flurer and Zucker (1988) observed coprophagy in marmosets fed a diet lacking in histidine and arginine, but did not observe coprophagy in marmosets fed a diet of the same protein content that contained both histidine and arginine. Histidine is an essential AA for one-carbon unit metabolism, protein biosynthesis, formation of major dipeptides in skeletal muscle and the brain such as carnosine, and conversion to histamine by decarboxylation (Wu 2013). Histidine can cross the blood-brain barrier like most AAs. Paradoxically, elevated levels of histidine and homocarnosine have been detected in the brains of rats, guinea pigs and infant monkeys that experience protein malnutrition (Taylor and Snyder 1972; Enwonwu and Worthington 1973) likely due to enhanced intramuscular protein and peptide hydrolysis. In protein-deficient monkeys, elevated levels of histidine in the brain were accompanied by decreased levels of arginine, threonine, isoleucine, leucine, and valine in their plasma, which compete with histidine to cross the blood-brain barrier (Enwonwu and Okolie 1983). Along with histidine, histamine levels in the brain were also increased in protein-deficient monkeys (Enwonwu and Okolie 1983). Histamine in the brain acts as a regulator of central acetylcholine secretion (He and Wu 2020). Protein deficiency and a specific AA deficiency may lead to impaired thermoregulation, elevated plasma levels of cortisol, reduced plasma levels of growth hormone, edema, and psychomotor dysregulation in primates (Enwonwu and Okolie 1983).

12.5 Dietary Requirements of Captive Carnivores, Herbivores and Omnivores for AAs

Animals have dietary requirements for AAs, but not protein (Wu 2016). Traditional methods to formulate diets for mammals (Bergen 2020; Oberbauer and Larsen 2020; Wu et al. 2014; Zhang et al. 2020), birds (He et al. 2020), crustaceans (Li et al. 2020b), and fish (Li et al. 2020c) have been based on the dietary CP content, which includes AAs, as well as non-protein and non-AA nitrogen. Data on dietary CP content may provide some clues into the requirements of zoo animals for dietary protein and AAs. For example, in summarizing the consensus agreement of the Giraffe Nutrition Workshop in 2005, Schmidt and Schlegel (2005) thoughtfully stated that "given the nutrient requirements of domestic ruminants and diet studies of wild giraffe, there is no nutritional reason to expect that the total dietary CP requirement of a mature giraffe is more than 12% of the complete diet (DM basis) when DM intake is at least 1.2% of the animal's body weight. Diets containing 10 to 14% CP (DM basis) will likely provide the maintenance needs of adult giraffe." The maintenance needs should include those for: (a) AAs that are irreversibly lost through catabolism, as well as excretion via the skin, urine and feces; and (b) AAs that are required for regulating immune and antioxidative responses, as well as the integrity of tissues such as the gastrointestinal tract, liver, eyes, heart, brain, and the skin. Because some non-protein and non-AA nitrogen (e.g., added melamine) may have no nutritive value and even be toxic to animals, and because AAs in feedstuffs can now be analyzed readily by advanced methods, such as high-performance liquid chromatography (Dai et al. 2014), dietary

AAs, instead of CP, should be recommended for zoo animals for their optimal growth, development, lactation, reproduction, and health. Because there are differences in digestion and metabolism of nutrients among carnivores, herbivores and omnivores, as noted previously, these animals likely have very different patterns of requirements for dietary AAs.

To date, little information is available regarding dietary requirements of zoo animals (including nonhuman primates) for AAs. Domestic animals (e.g., pigs, chickens, and sheep) may be used to assess the digestibility of AAs in proteins of commercially available avian and mammalian whole prey diet items targeted for consumption by zoo animals (e.g., Kerr et al. 2014). In addition, model animals can be used to estimate the nutrient requirements of captive animals with similar digestive physiology and metabolism (Edwards 2003). Furthermore, data from human studies (Wu 2016; Young and Borgonha 2000) can be based to recommend the requirements of nonhuman primates for dietary AAs. Diets should be optimal for the growth, development, reproduction, survival and health of all animals. These common criteria should be used for defining dietary requirements of various species of zoo animals for AAs. However, it should be borne in mind that additional criteria for recommending nutrient requirements for domestic animals (e.g., growth performance, feed efficiency, and productivity) may be different from those for zoo animals (e.g., longevity and social behavior).

Based on work with swine and poultry, as well as companion animals (Baker and Czarnecki-Maulden 1991), the "ideal protein" has been considered to optimize the provision of EAAs for zoo animals, including carnivores (Dierenfeld et al. 2011). Because this nutritional concept does not take into consideration the AAs that are synthesized in animal cells, we must think "out of the box" to recommend that the diets of carnivores, like other animal species (Wu 2014), include all proteinogenic AAs. According to the review of AA composition in common raw meats from domestic (e.g., beef, chicken, horse, pork, and turkey) and "wild" (e.g., antelope, bison, boar, guinea fowl, and rabbit) animals, Dierenfeld et al. 2011 stated that arginine, leucine, methionine plus cysteine, and phenylalanine plus tyrosine are limiting in all meats examined, regardless of source, compared to requirements established for obligate carnivores. However, it remains uncertain whether or not the previously recommended dietary requirements of the animals for the reference AA "lysine" and other EAAs are accurate, because tissue-specific metabolism of all EAAs can be affected by the dietary intakes of so-called "nutritionally nonessential AAs" that are not included in the "ideal protein" (Wu 2013). It is unlikely that animal meats would not meet the requirements of carnivores for dietary AAs. In the wild, a carnivore eats whole prey animals (including such internal organs as the liver, kidneys and heart). Thus, it is more appropriate to estimate AA requirements of carnivores on the basis of the composition of AAs in the whole body rather than meat. This does not mean that zoo carnivores should be fed the whole carcasses of prey animals due to concerns over food safety. The composition of AAs in the bodies of various species of animals (mammals, birds and fish) is similar (Wu 2013, 2018). In contrast to the previously analyzed meats (Dierenfeld et al. (2011), the animal body and animal-source feedstuffs (e.g., chicken by-product meal and poultry by-product meal) provide more arginine and leucine than lysine (Li and Wu 2020; Wu 2013; Wu et al. 2016). Chicken viscera digest and spray-dried peptone from enzyme-treated porcine mucosal tissues supply more leucine than lysine (Li and Wu 2020). As shown in Table 12.1, all alternative animal protein products contain a large amount of taurine and proteinogenic AAs [particularly arginine, glutamate, glutamine, glycine, proline, 4-hydroxyproline, serine, sulfur-containing AAs (methionine, cysteine and taurine), and tryptophan] that are crucial for intestinal integrity and health, one-carbon metabolism, anti-oxidative reactions, and immune responses in all tissues of the animals (Hou et al. 2015; Liu et al. 2020; Wang et al. 2013, 2020; Wu et al. 2019; Zhang et al. 2019). In addition, meat provides creatine that is essential for muscular and neurological development (Wu 2010).

Table 12.1 Content of total amino acids (peptide-bound plus free amino acids) in the whole body of pigs and in animal-derived feedstuffs[a]

	Pig body		CBPM		PBM (PFG)		CVD		SDPM	
Amino acid (AA)	AA content (% of DM)	% of lysine (g/g)	AA content (% of DM)	% of lysine (g/g)	AA content (% of DM)	% of lysine (g/g)	AA content (% of DM)	% of lysine (g/g)	AA content (% of DM)	% of lysine (g/g)
Ala	3.00	109	4.63	100	4.11	112	4.42	82.2	3.95	86.3
Arg	3.09	112	4.85	105	4.28	117	4.31	80.1	4.05	88.3
Asn	1.64	59.7	2.66	57.6	2.65	72.3	2.68	49.8	1.71	37.3
Asp	195	71.0	4.01	87.0	3.99	109	3.93	72.9	4.19	91.4
Cys[b]	0.60	21.9	1.09	23.6	1.08	29.4	1.31	24.2	1.11	24.2
Gln	2.34	84.9	3.96	85.9	3.52	96.3	4.00	74.2	3.14	68.5
Glu	3.86	140	5.45	118	4.91	134	6.80	126	6.50	142
Gly	5.36	195	6.06	131	7.09	194	8.85	164	5.58	122
His	0.95	34.4	1.39	30.0	1.36	37.0	0.80	14.8	1.45	31.6
Hyp	1.73	62.9	1.89	41.0	2.32	63.4	1.86	34.5	0.89	19.4
Ile	1.61	58.6	2.77	60.2	2.46	67.1	4.12	76.4	2.75	60.1
Leu	3.12	113	5.38	117	4.47	122	6.55	122	4.85	106
Lys	2.75	100	4.61	100	3.66	100	5.39	100	4.58	100
Met	0.85	31.0	1.46	31.6	1.43	39.0	1.70	31.5	1.35	29.5
Phe	1.56	56.8	2.75	59.7	2.40	65.5	3.97	73.7	2.63	57.3
Pro	3.93	143	4.39	95.1	5.24	143	5.93	110	3.56	77.8
Ser	2.02	73.5	3.11	67.5	2.71	74.0	6.92	129	3.80	82.9
Thr	1.60	58.1	2.83	61.3	2.64	72.2	2.14	39.7	3.21	70.1
Trp	0.51	18.4	0.77	16.8	0.65	17.8	1.10	20.4	0.71	15.4
Tyr	1.24	45.0	2.33	50.6	1.94	53.1	2.75	51.0	2.52	55.0
Val	1.93	69.9	3.39	73.5	3.01	82.1	5.97	111	3.43	74.9
TPAA	45.7	–	69.8	–	65.9	–	85.5	–	66.0	–
Taurine	0.14	–	0.21	–	0.40	–	0.14	–	0.18	–

[a]Adapted from Wu et al. (2013) for the 30-day-old pig and from Li and Wu (2020) for the animal-derived feedstuffs. The molecular weights of intact amino acids were used for the calculation of AA content in the pig body and the feedstuffs
[b]Cysteine + ½ cystine

CBPM chicken by-product meal, *CVD* chicken visceral digest, *DM* dry matter, *Hyp* 4-hydroxyproline, *PBM (PFG)* poultry by-product meal (pet-food grade), *SDPM* spray-dried peptone from enzymes-treated porcine mucosal tissues, *TPAA* total proteinogenic amino acids

Based on the AA content of the pig body (Wu 2013) and diets for domestic animals [e.g., sheep (a herbivore ruminant; Satterfield et al. 2013), swine (an omnivore mammal; Wu et al. 2011), and chicken (an omnivore bird; He et al. 2020; Wu 2014), we recommend the requirements of captive carnivores (young and adult; Table 12.2), herbivores (young and mature; Table 12.2), and omnivores (young, adult and lactating mammals; as well as young and mature birds; Table 12.3) for dietary true protein and AAs as percentages of the total diet. Similarly, data on the requirements of crustaceans (Li et al. 2020b) and fish (Li et al. 2020c) for dietary AAs in aquaculture can serve as useful references to formulate diets for these classes of animals in the zoo. As reported by Hou et al. (2016), the ratios of AAs to lysine in animal diets differ from those in the animal body to various extents, depending on individual AAs. This is because dietary AAs are degraded by the small intestine at different rates during the first pass and AAs in plasma are utilized by the whole body at different rates (Wu 2013). The recommendations based on AA composition in the body provides an initial framework for feeding practices and further studies. As an animal becomes older, its rate of metabolism (including basal protein metabolism) per kg body weight decreases (Wu 2018). However, this also includes reductions in the conversion of

Table 12.2 Recommended requirements of zoo carnivores and herbivores for dietary amino acids[a]

	Carnivores		Herbivores (adult)		Herbivores (young)[b]	
Amino (AA)	AA content in diet (% of DM)	% of lysine in diet (g/100 g)	AA content in diet (% of DM)	% of lysine in diet (g/100 g)	AA content in diet (% of DM)	% of lysine in diet (g/100 g)
Ala	3.00	109	0.93	131	1.30	131
Arg	3.09	112	0.84	119	1.18	119
Asn	1.64	59.7	0.73	103	1.02	103
Asp	195	71.0	0.83	117	1.16	117
Cys	0.60	21.9	0.27	37.5	0.37	37.5
Gln	2.34	84.9	1.29	181	1.80	181
Glu	3.86	140	1.12	158	1.57	158
Gly	5.36	195	0.70	98.4	0.98	98.4
His	0.95	34.4	0.31	43.8	0.43	43.8
Hyp	1.73	62.9	–	–	–	–
Ile	1.61	58.6	0.60	84.4	0.84	84.4
Leu	3.12	113	1.19	167	1.66	167
Lys	2.75	100	0.71	100	0.99	100
Met	0.85	31.0	0.23	32.8	0.33	32.8
Phe	1.56	56.8	0.70	98.4	0.98	98.4
Pro	3.93	143	1.13	159	1.58	159
Ser	2.02	73.5	0.72	102	1.01	102
Thr	1.60	58.1	0.54	76.6	0.76	76.6
Trp	0.51	18.4	0.18	25.0	0.25	25.0
Tyr	1.24	45.0	0.53	75.0	0.75	75.0
Val	1.93	69.9	0.71	100	0.99	100
TPAA	45.7	–	14.3	–	20.0	–
Taurine	0.10	–	0.00	–	0.02	–

[a]Vaues are AA content in diet. The molecular weights of intact amino acids are used for the calculation of AA content in the diet. Intakes of dry matter by zoo animals range from 1% to 6% of their body weight, depending on species, age, and physiological state

[b]Before the normal weaning age. Note: within the first 1 month after weaning, the dietary content of all amino acids is reduced by 10%. A high intake of dietary protein in post-weaning mammals increases risks for intestinal dysfunction

DM dry matter; *Hyp* 4-hydroxyproline, *TPAA* total proteinogenic amino acids

phenylalanine into tyrosine and of methionine into cysteine in older animals than in younger animals. Consequently, much attention should be paid to adequate dietary intakes of both tyrosine and cysteine by ageing animals. Although adult animals gain little protein in the body or have a reduced requirement for dietary lysine, their small intestine still requires a relatively large amount of dietary threonine to produce mucins for intestinal protection. Likewise, adults also need dietary tryptophan for the production of bioactive metabolites (e.g., serotonin, melatonin, and indoles) to maintain neurological and intestinal functions. Thus, compared with young nonruminants, the dietary ratios of cysteine, tyrosine, threonine and tryptophan to lysine for adult ruminants may be greater (e.g., +10% for cysteine/lysine and tyrosine/lysine; +12% for threonine/lysine and tryptophan/lysine; Wu 2018). However, this may not be true for ruminants, because the ability of their rumen to synthesize cysteine, tyrosine, threonine and tryptophan in adults is greater than that in the young ruminant.

Intakes of DM by zoo animals range from 1% to 6% of their body weight, depending on species, age, and physiological state. For example, within the same given species, young animals have a greater metabolic rate and, therefore, consume more feed per kg body weight, compared with adults (Wu 2018). Likewise, at the same relative developmental stage, birds have a greater metabolic rate and, therefore, consume more feed per kg body weight, compared with ruminants

Table 12.3 Recommended requirements of mammalian and avian omnivores in zoos for dietary amino acids[a]

	Mammalian omnivores						Avian omnivores			
	Mammals (adults)		Mammals (young)[b]		Mammals (lactating)		Birds (adults)		Birds (young)	
Amino acid (AA)	AA content in diet[c] (% of DM)	% of lysine in diet (g/g)	AA content in diet[d] (% of DM)	% of lysine in diet (g/g)	AA content in diet[c] (% of DM)	% of lysine in diet (g/g)	AA content in diet[c] (% of DM)	% of lysine in diet (g/g)	AA content in diet[c] (% of DM)	% of lysine in diet (g/g)
Ala	0.81	97.4	1.38	95.6	1.05	104	0.90	102	1.36	102
Arg	0.83	100	1.44	99.8	1.73	171	0.95	109	1.41	105
Asn	0.57	68.5	0.97	67.1	0.83	82.5	0.49	56.2	0.75	56.1
Asp	0.81	97.4	1.38	95.6	1.19	118	0.58	66.3	0.89	66.2
Cys	0.25	30.4	0.39	26.8	0.33	32.5	0.32	36.4	0.43	32.1
Gln	1.26	152	2.17	151	1.74	173	1.13	129	1.72	128
Glu	1.41	170	2.42	168	2.29	226	1.57	179	2.38	178
Gly	0.90	108	1.53	107	0.95	93.8	1.56	177	2.35	175
His	0.33	39.6	0.56	38.6	0.49	48.8	0.31	35.2	0.47	35.1
Ile	0.54	65.4	0.94	65.4	0.83	82.5	0.61	69.3	0.92	68.7
Leu	1.10	132	1.90	132	1.78	176	0.96	110	1.46	109
Lys	0.83	100	1.44	100	1.01	100	0.88	100	1.34	100
Met	0.25	30.4	0.39	26.8	0.32	31.3	0.37	42.2	0.54	40.1
Phe	0.61	73.0	1.04	72.1	0.97	96.3	0.53	60.3	0.81	60.2
Pro	0.96	116	1.64	114	1.57	155	1.63	185	2.46	184
Ser	0.49	59.3	0.85	58.7	0.93	92.5	0.61	69.3	0.93	69.2
Thr	0.58	70.0	0.89	62.1	0.71	70.0	0.62	70.3	0.90	67.2
Trp	0.18	21.3	0.27	18.5	0.23	22.5	0.15	17.0	0.22	16.0
Tyr	0.47	56.3	0.81	56.2	0.78	77.5	0.40	45.2	0.60	45.1
Val	0.59	71.5	1.03	71.3	0.91	90.0	0.71	80.3	1.07	79.9
TPAA	13.8	–	23.4	–	20.6	–	15.3	–	23.0	–
Taurine	0.00	–	0.05	–	0.00	–	0.00	–	0.00	–

[a]Vaues are AA content in diet. The molecular weights of intact amino acids are used for the calculation of AA content in the diet. Intakes of dry matter by zoo animals range from 1% to 5% of their body weight, depending on species, age, and physiological state

[b]Before weaning. Note: Within the first month after weaning, the dietary content of all amino acids is reduced by 10%. A high intake of dietary protein in post-weaning mammals increases risks for intestinal dysfunction

[c]The true digestibility of amino acids in dietary protein and the content of dry matter in the diet are assumed to be 88% and 90%, respectively

[d]The true digestibility of amino acids in dietary protein and the content of dry matter in the diet are assumed to be 92% and 90%, respectively

DM dry matter; *TPAA* total proteinogenic amino acids

(Wu 2018). Because embryos and fetuses are particularly sensitive to ammonia concentrations in blood (Herring et al. 2018), high intakes of dietary protein are not recommended for females before breeding or during early gestation. Diets for dams during late gestation can be the same as those for early gestation. However, as the fetus grows rapidly during the last trimester of pregnancy, the amount of the diet fed to the dams can be increased appropriately (e.g., by 20 to 25% over that during early gestation). Based on studies with swine (Wu et al. 2017, 2018), dietary supplementation with arginine (e.g., 0.4% of the diet) shortly before the implantation of blastocysts can be beneficial for reducing the concentrations of ammonia in plasma, enhancing placental angiogenesis, and improving embryonic/fetal survival in zoo animals.

Our recommended values for dietary AA requirements for zoo carnivores, herbivores and omnivores may not be optimum for all AAs and all animal species, but they are expected to serve as

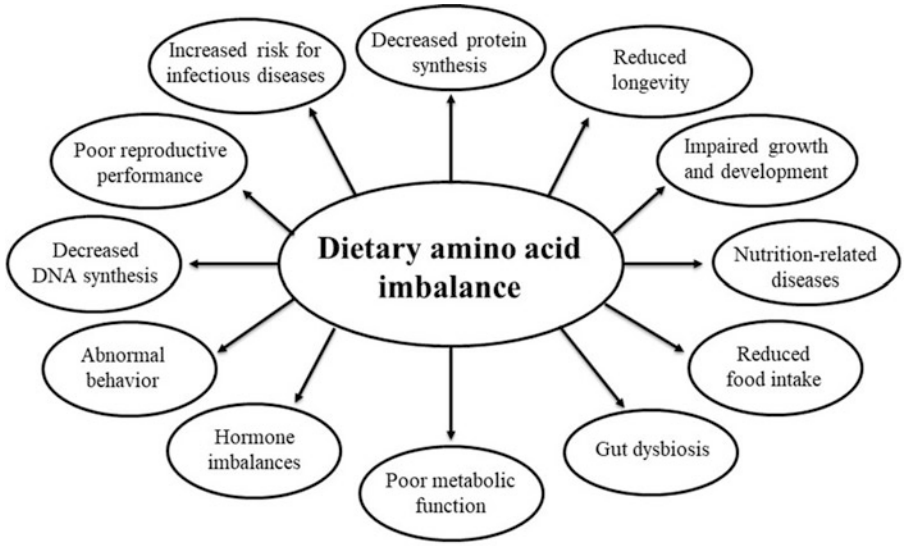

Fig. 12.5 Consequences of dietary amino acid (AA) imbalances in zoo animals. Amino acids are essential for the maintenance, growth, development, health, and survival of all animals, including those in the zoo. Inadequate AA nutrition or excessive intake of AAs can lead to nutrition-related diseases, impaired immunity, as well as the dysregulation of necessary physiological and metabolic functions in carnivores, herbivores, and omnivores. The diets of zoo animals should contain optimum balances and amounts of all proteinogenic amino acids. Taurine must be included in the diets of carnivores that do not synthesize this nonproteinogenic amino acid

helpful guidelines for feeding practices and future research, as noted previously. Because the metabolism of animals is affected by physiological, environmental and pathological factors, their optimum requirements for dietary AAs are not one set of fixed data, and may undergo dynamic changes with changing conditions. This calls for a range of the recommended requirement values, which need to be modified under practical feeding conditions. Therefore, the data in Tables 12.2 and 12.3 should be considered only as references and revised as new research findings become available.

12.6 Conclusion

In summary, domestic livestock species with established dietary nutrient requirements provide a baseline to use as a reference in formulating dietary requirements for exotic zoo animals since the processes used to determine dietary nutrient requirements are not practical for zoo animal species. However, it is important to take into account the major differences between domestic and wild species that could influence dietary nutrient requirements such as habitat, diet, behavior, and physiology. Malnutrition of protein and AAs can lead to many different nutrition-related diseases and disorders that may threaten the vitality and fecundity of zoo animal species (Fig. 12.5). Zoo animals will not thrive in captivity if their health is not optimal. Especially for endangered species, it is imperative that captive populations successfully thrive in order to conserve the Earth's biodiversity. Therefore, adequate provision of dietary AAs is crucial for successful management, sustainability and expansion of all zoo animals, including captive carnivores, herbivores and omnivores.

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