Ecology of Vertebrate Nutrition

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Vertebrate nutritional ecology is the study of the interrelationships between food resources in the environment and the consumptive use of these food resources by vertebrate animals. Consumptive use includes how vertebrate animals procure, digest, absorb and metabolise available foods in the environment to satisfy their requirements for health, growth and reproduction. The challenge for wild vertebrates is to satisfy their nutritional requirements in an environment that often varies in food availability and quality. Vertebrate animals have evolved a diverse and interesting suite of solutions to the problem(s) of acquiring necessary nutrients and energy in a world where food often does not want to be eaten.

Vertebrate Nutritional Needs

All vertebrates require certain amounts of energy, protein and 'essential' nutrients. Dietary sources of energy include carbohydrates, protein and fat. Dietary protein is necessary for satisfying an animal's protein requirements. Certain dietary nutrients are classified as 'essential' because they are required for synthesis or functioning of crucial chemical compounds, yet they cannot be synthesised by the organism in sufficient amounts to satisfy requirements. Thus, essential nutrients must come from diet. For most birds and mammals, about 38 nutrients are required in the diet including 10 essential amino acids, 1–3 essential fatty acids, 13 vitamins and at least 14 essential minerals

(Robbins, 1993; Murphy, 1996; Barbosa *et al.*, 2009). **See also**: Animal Nutrient Requirements; Lipids; Vertebrata (Vertebrates)

Energy requirements

The energy requirements of the animal and the energy density of the food primarily determine the amount of food eaten by an animal. Energy requirements of an animal change to some extent with environmental temperature depending on the thermoregulatory capacity of the animal. Energy requirements increase with activity and during periods of production (e.g. growth, storage and reproduction). However, metabolism and energy use continues even when an animal is at rest. Resting metabolic rate of a bird or mammal can be predicted from its body mass using the following equations (Robbins, 1993): **See also**: Allometry and Metabolic Scaling in Ecology; Ecological Consequences of Body Size; Ecology of Storage and Allocation of Resources: Animals; Energy Cycle in Vertebrates; Thermoregulation in Vertebrates; Vertebrate Metabolism

$$\text{Passerine birds}: Y = 114.8(X)^{0.726}$$

$$\text{Nonpasserine birds}: Y = 73.5(X)^{0.734}$$

$$\text{Eutherian (or placental) mammals}: Y = 57.2(X)^{0.716}$$

$$\text{Marsupial mammals}: Y = 46.6(X)^{0.737}$$

In the above equations, Y is resting metabolic rate in kilocalories per day, and X is body weight in kilograms. The similar exponents suggest a common allometric relationship between metabolic rate and body size in these vertebrates. The nutritional implication of this allometric relationship (with an exponent of about 0.72) is that larger animals have lower energy requirements per unit body weight than smaller animals. In addition, the higher value of the multiplication constant in birds compared to mammals demonstrates that birds have higher energetic costs

for a given body size than mammals. For example, using the equations above, a 2 kg nonpasserine bird such as a goose would require 122 kcal day^{-1} to satisfy the energy costs of resting metabolic rate compared to only 94 kcal day^{-1} (or about 25% less) for a similar-sized placental mammal such as a snowshoe hare (*Lepus americanus*). **Table 1** includes measured values of resting metabolic rate for selected birds and mammals of a variety of types and sizes. **See also**: Vertebrate Metabolic Variation

The additional energy required to fuel the costs of thermoregulation, activity and production are also important in determining the total energy requirements of an animal. Each of these costs can be estimated separately and then summed to estimate total energy requirements for the animal, although most such estimates use captive animals in various degrees of restraint, which poses many problems. Recently, nutritional ecologists have used isotopes of hydrogen and oxygen to label the metabolic water of free-living animals. Using the relative change over time in concentration of hydrogen and oxygen isotopes in the metabolic water of the animal, an estimate of the total energy requirements of a free-living animal is obtained (called 'field metabolic rate'). Studies using this so-called 'doubly labelled water method' have revolutionised our understanding of energy requirements of wild and captive animals (Speakman, 1997).

Protein and amino acid requirements

Proteins are amino acids bound together by peptide bonds. Dietary protein can be used as a source of body protein, fat or carbohydrate whereas dietary fat or carbohydrate alone cannot be used to increase the net amount of body protein. Hence, insufficient dietary protein has serious

Table 1 Resting metabolic rate of selected vertebrates as a function of their body mass

Species	Body mass (kg)	Resting metabolic rate (kcal day^{-1})	Resting metabolic rate per unit body mass (kcal kg^{-1} day^{-1})
Passerine birds[a]			
House wren (*Troglodytes aedon*)	0.009	5.3	588.9
Common raven (*Corvus corax*)	0.866	94.9	109.6
Nonpasserine birds[a]			
Ruby-throated Hummingbird (*Archilochus colubris*)	0.003	1.6	533.3
Great Horned Owl (*Bubo virginianus*)	1.450	108.0	74.5
Trumpeter Swan (*Cygnus buccinator*)	8.880	418.0	47.1
Ostrich (*Struthio camelus*)	100.0	2350.0	23.5
Eutherian mammals[b]			
Mouse (*Mus musculus*)	0.0250	4.7	188.0
Domestic Dog	11.7	445.8	38.1
Human (*Homo sapiens*)	70.0	1700.4	24.3
Elephant (*Elephas maximus*)	3833.0	30 873.6	8.1
Marsupial mammals[c]			
Fat-tailed mouse (*Sminthopsis crassicaudata*)	0.014	2.2	157.1
Sugar glider (*Petaurus breviceps*)	0.128	10.2	79.7
Tammar wallaby (*Macropus eugenii*)	4.796	159.4	33.2
Red kangaroo (*Megaleia rufa*)	32.490	642.7	19.8

[a]From Lasiewski and Dawson (1967).
[b]From Schmidt-Nielsen (1997).
[c]From Dawson and Hulbert (1970).

consequences because of inadequate synthesis of body protein. Of the 20 or so common amino acids, animals without significant fermentative capacity usually require 10 essential amino acids including arginine, histidine, iso-leucine, leucine, threonine, lysine, methionine, phenyl-alanine, tryptophan and valine. Cats have lost the ability to synthesise taurine and so they also require this amino acid in their diet. Animals with significant fermentative capacity probably have similar amino acid requirements as non-fermenting animals. However, the protein produced by gut microbes during fermentation and subsequently digested and absorbed by the herbivore effectively eliminates the need for dietary sources of essential amino acids.

Protein requirements depend on the physiological state of the animal. For example, protein requirements are highest in growing animals and generally decline with age. Protein requirements of adults increase during productive periods such as egg-laying in birds or during lactation in mammals. The quantity of protein required by an animal also depends on the energy density of the diet and the amino acid composition of dietary protein. If there is a shortage of dietary fat or carbohydrate, then some protein must be used to satisfy energy requirements so that all dietary protein is not available to satisfy protein require-ments of the animal. For animals without significant fer-mentative capacity, amino acid composition of dietary protein must provide a balanced profile of essential amino acids relative to need so that normal rates of protein syn-thesis are maintained. If dietary availability of an essential amino acid is deficient, then rate of protein synthesis will decline and other amino acids not used in protein synthesis will quickly be catabolised.

Carbohydrate and fat requirements

Carbohydrates and fats are the primary energy sources in most vertebrate diets. Dietary requirements for specific carbohydrates and fats are less exacting than for proteins. Carbohydrates are a biochemically diverse group of com-pounds that vary widely in how completely they can be digested by vertebrates. For example, the most abundant forms of carbohydrate in plants are cellulose and starch. Vertebrates lack cellulase, the digestive enzyme that digests cellulose, and so cellulose is either not utilised at all or must be digested by gut microbes during fermentation. **See also**: Cellulose: Structure and Distribution; Starch and Starch Granules

Vertebrate animals can grow normally on a diet without carbohydrates provided sufficient triglycerides are avail-able for satisfying energy requirements. In contrast, a few specific fats are required in the diet of vertebrates. Three fatty acids (linoleic, linolenic and arachidonic acid) are usually categorised as essential for vertebrates, although current evidence suggests that linoleic acid is the only essential fatty acid in birds (Klasing, 1998). Essential fatty acids are important as precursors for prosta-glandin synthesis and as structural components in cell membranes. **See also**: Fatty Acids: Structures and Properties; Gluconeogenesis; History of Fatty Acids; Polysaccharides: Energy Storage

Vitamins and mineral requirements

Vitamins and minerals are often referred to as micro-nutrients because they are required in small quantities compared to macronutrients such as protein, carbo-hydrates and fats. Animals require at least 14 minerals, including macroelements (e.g. calcium, phosphorus, sodium, potassium, magnesium, chlorine and sulfur), which are needed in relatively large amounts (milligrams per gram of food intake), and trace elements, which are needed in relatively small amounts (e.g. iron, zinc, manganese, copper, molybdenum, iodine, selenium, cobalt, fluoride and chromium). **See also**: Phosphorus Availability in the Environment; Sodium, Calcium and Potassium Channels

Most vertebrates without significant fermentative cap-acity require 13 vitamins: fat-soluble vitamins include vitamins A, D, E and K; water-soluble vitamins include thiamin (B_1), riboflavin (B_2), pyridoxal (B_6), nicotinamide (B_7), pantothenic acid, biotin, folic acid, cyanocobalamin (B_{12}) and choline. Fat-soluble vitamins can usually be stored in the animal so that deficiencies are extremely rare in free-living individuals. Excesses of fat-soluble vitamins, especially vitamins A and D, can be extremely toxic. In contrast, most water-soluble vitamins cannot be stored and excesses are excreted, although some vitamin B_{12} and riboflavin can be stored in the liver. Thus, a regular dietary supply of water-soluble vitamins is needed to satisfy vita-min requirements of vertebrates. Water-soluble vitamins primarily function as precursors for coenzymes. Deficien-cies include growth retardation, dermatitis, poor fea-thering or fur and reduced reproductive output. **See also**: Vitamin A Deficiency; Vitamin B_{12}: Disorders of Absorp-tion and Metabolism; Vitamin B_2 Deficiency; Vitamin D Deficiency; Vitamin E Deficiency; Vitamin K: Structure and Function

In addition to these 13 vitamins required of most ver-tebrates, vitamin C is required in the diet of many ver-tebrates including all fish, and some mammals (e.g. bats, guinea-pigs and some primates and cetaceans). Other ver-tebrates synthesise vitamin C in the kidney (e.g. amphib-ians, reptiles, monotremes and most nonpasserine birds) or in the liver (e.g. most mammals). About one-half of pas-serine birds can synthesise vitamin C in the liver whereas other passerine birds are unable to synthesise this vitamin and thus must satisfy requirements entirely from dietary sources. **See also**: Amphibia; Chiroptera (Bats); Primates (Lemurs, Lorises, Tarsiers, Monkeys and Apes); Vitamin C Deficiency

Gut microbes synthesise some vitamins. For example, bacteria in the digestive tract of mammals synthesise vita-mins K and B_{12}. Such symbiotic synthesis of vitamins is particularly important for foregut fermenting herbivores such as ruminants because it makes these animals inde-pendent of a dietary source of these vitamins. Although gut microbes in hindgut fermenting herbivores may also

synthesise vitamins, coprophagy may be necessary for the herbivore to utilise these vitamins produced by microbes in the hindgut. **See also**: Vertebrate Herbivory and Its Ecosystem Consequences

Procuring Food

Much of the daily activity of vertebrate animals is associated with obtaining an adequate quantity and quality of food. Vertebrates use a diversity of methods for obtaining food. The largest living vertebrate, the blue whale, and other plankton-eating whales use filtering devices called baleens to filter large volumes of water and capture the small plankton in hair-like filaments on horny plates. Other filter-feeding vertebrates include many pelagic fish (e.g. herring and mackerel), large sharks (e.g. basking and whale sharks) and even a few birds (e.g. petrels, flamingos and many ducks). **See also**: Biomechanical Studies of Food and Diet Selection

The majority of vertebrates procure food that is much larger than plankton and these larger masses of food must be captured and manipulated differently from small particles such as plankton. Most mammals mechanically break down food using teeth, whereas birds have no teeth and use a specialised portion of their stomach, the gizzard, for this purpose. Bill morphology in birds, and tooth and jaw structure in all other vertebrate classes are impressively diverse and provide excellent examples of evolutionary design in relation to procuring food. For example, dagger-like bills of herons capture fast-moving aquatic prey, serrated bills of mergansers seize and hold fish, spatula-like bills of spoonbills and shovellers filter small aquatic invertebrates, raptorial bills of falcons, hawks and eagles shred prey, chisel-shaped bills of woodpeckers uncover wood-boring insects and conical bills of many songbirds crack open seeds. Adaptations of the teeth, jaws and jaw musculature are closely related to the specific styles of feeding in nonavian vertebrates and especially in mammals. For example, the structure of molar teeth includes blade-like molars in carnivores that shear, molars with rounded cusps in omnivores that crush and grind and molars with ridged cusps in herbivores that finely section and grind plants. Similarly, chisel-like incisors in rodents and rabbits are used for gnawing, dagger-like canines of most carnivorous mammals are used for piercing and tearing food. The arrangement and types of teeth in mammals allow them to masticate or chew their food, an ability relatively unique among vertebrates. **See also**: Ingestion in Birds; Ingestion in Mammals

Muscular, Acidic Stomach in Macrophagous Food Processing

Most vertebrate food consists of proteins, fats and carbohydrates, which are large molecules that must be broken down into simpler units so they can be absorbed and utilised by the vertebrate (Karasov and Martinez del Rio,

2007). In vertebrates, this breakdown takes place primarily in the stomach and midgut using both mechanical and chemical processes. **See also**: Vertebrate Food Pathway and Gut: Overview

Mechanical processes in the stomach involve contraction of circular and longitudinal muscle layers in the stomach wall that mixes the food, saliva and stomach secretions. The stomach initiates chemical digestion of protein by secreting enzymes such as pepsinogen and hydrochloric acid. The stomach of most birds is divided into a proventriculus, where chemical digestion is initiated, and a gizzard, where ingested food is mechanically mixed and ground (replacing the function of teeth). Often small, hard objects such as pebbles are swallowed by herbivorous birds to aid in the grinding of food in the gizzard. **See also**: Digestive System of Amphibians, Reptiles and Birds; Digestive System of Mammals

Specificity of Vertebrate Digestive Enzymes

Before protein, fats and carbohydrates can be absorbed and utilised, they must be broken down into simpler building blocks of amino acids, esters of fatty acids and glycerol, and simple sugars (e.g. glucose, sucrose), respectively. In vertebrates, the chemical breakdown of ingested food involves digestive enzymes that increase the rate of hydrolysis, adding H^+ to one part of the large food molecule and OH^- to the other part. Hydrolysis of chemical bonds divides the larger food molecules into their simpler building blocks that can then be absorbed.

Digestive enzymes are proteins produced by cells of the stomach, intestine and pancreas that regulate the rate of chemical breakdown of food compounds. Like all enzymes, digestive enzymes are to some degree specific for a certain substrate or reactant molecule, and the activity of digestive enzymes is sensitive especially to temperature and pH. Some digestive enzymes hydrolyse certain chemical bonds regardless of their location in a molecule and so may act on many different substrates. For example, trypsin and chymotrypsin catalyse the hydrolysis of peptide bonds in any protein in which the carboxyl group is part of certain amino acids. Other digestive enzymes are much more specific and hydrolyse certain chemical bonds in one location in certain molecules. For example, sucrase (sucrose α-glucosidase) catalyses hydrolysis of the disaccharide sucrose into glucose and fructose, and cannot hydrolyse the same chemical bond in other disaccharides such as lactose and maltose (these disaccharides are digested by their own specific enzymes, lactase (β-D-galactosidase) and maltase (α-glucosidase) (Karasov and Martinez del Rio, 2007).

Proteases

Each of the three major types of foodstuffs has a corresponding group of enzymes associated with its digestion:

proteases for digestion of protein, carbohydrases for digestion of carbohydrates and lipases for digestion of fats. Proteases include endopeptidases that catalyse hydrolysis of peptide bonds located well within the protein molecule, and exopeptidases that catalyse hydrolysis of peptide bonds near the end of a peptide chain. Thus, digestion of food protein involves endopeptidases such as pepsin, trypsin and chymotrypsin, which break large peptide chains into shorter polypeptide segments, and then exopeptidases such as carboxypeptidase and aminopeptidase, which break down the shorter polypeptide segments into free amino acids and di- or tripeptides. **See also**: Proteases

To avoid digestion of their own body protein, vertebrates produce many proteolytic enzymes as zymogens, inactive forms of the digestive enzyme that become active at specific (usually low) pH or by interaction with another specific enzyme. For example, protein digestion usually begins in the stomach with secretion of pepsinogen, which is later converted to pepsin in the highly acidic environment of the stomach.

Carbohydrases

Carbohydrases include polysaccharidases (e.g. amylases), which hydrolyse the glycosidic bonds of long-chain carbohydrates such as starch, and glycosidases (e.g. sucrase, lactase and maltase) which hydrolyse a specific glycosidic bond in certain disaccharidases. Amylase is secreted by the vertebrate pancreas and in the saliva and is located primarily in the stomach. In contrast, most glycosidases are located in the intestinal mucosa. **See also**: Polysaccharides

Lipases

Lipases, which are responsible for most of the chemical digestion of fats, act only at a lipid–water interface. Fats are water-insoluble and are rendered water-soluble by emulsification, a process involving the mixing of fat with detergents such as bile salts, secreted by the liver, and lecithin to form small droplets called micelles. Formation of micelles is necessary for fat digestion because it increases the surface area available for pancreatic lipase digestion. Lipases secreted by the pancreas break down triglycerides into fatty acids, monoglycerides and diglycerides that can be absorbed by the intestine. **See also**: Lipases: Digestion of Neutral Lipids; Physiological and Pathological Implications

Modulation of digestive enzyme activity in relation to diet

Activity of digestive enzymes in vertebrates, including pancreatic proteases, amylase and lipase as well as intestinal aminopeptidase, sucrase and maltase, generally changes in proportion to the amount of dietary substrate (i.e. protein-digesting enzymes increase with their respective dietary protein substrate, carbohydrate-digesting enzymes increase with their respective dietary carbohydrate substrate). Although this generalisation holds for laboratory rats, a fish (*Tilapia mossambica*), and poultry, the few wild birds studied to date exhibit somewhat different patterns of modulation in digestive enzymes (Karasov and Hume, 1997). Specifically, wild birds fed diets with higher carbohydrate concentrations did not increase their digestive disaccharidases, whereas birds fed diets with higher protein concentrations increased their aminopeptidase-N activity. This pattern of modulation of digestive peptidases but not disaccharidases holds across bird species that are dietary generalists and specialists, although more comparative studies are needed to determine if dietary flexibility is generally unrelated to this type of digestive plasticity.

Nutrient Absorption

Chemical digestion of proteins, fats and carbohydrates along with absorption of the end products of digestion primarily occurs in the small intestine. In the anterior small intestine (the duodenum) secretions from the liver and pancreas are delivered. In the posterior small intestine (the jejunum and ileum) digestion is completed and absorption takes precedence. Products of digestion are absorbed across the intestinal microvilli of the apical membrane of the absorptive cells and then move via blood circulation into the animal's tissues and cells. **See also**: Nutrient Acquisition, Assimilation and Utilization

Mechanisms of absorption

Absorption involves several processes including passive diffusion, facilitated diffusion and active transport (Karasov and Hume, 1997). Fat-soluble nutrients such as fatty acids and monoglycerides passively diffuse across the lipid bilayer intestinal membrane. Once fatty acids and glycerol are inside the absorptive cell they are reconstituted into triglycerides, collected together with other cellular lipids to form tiny droplets called chylomicrons and then exported to the blood by exocytosis. Water and small, water-soluble nutrients such as certain sugars and alcohols passively diffuse through water-filled pores in the intestinal membrane. Such passive diffusion of nutrients uses the energy of the concentration gradient and requires no cellular metabolic energy. Although all nutrients are probably absorbed passively to some extent, many nutrients are absorbed against a concentration gradient and this process, called active transport, requires cellular metabolic energy. Certain sugars and amino acids are actively transported across the intestinal membrane. **See also**: Vertebrate Food Pathway and Gut: Overview

Modulation of nutrient absorption rate in relation to diet

Absorption rate of dietary nutrients in the intestine of vertebrates provides strong evidence for adaptive modulation of digestive features in response to diet change (Karasov and Hume, 1997). Nutrient transport rates for glucose, vitamins and amino acids increases with dietary substrate in mammals. However, no modulation of nutrient transport rates for glucose has been observed in the four species of bird studied to date (McWilliams and Karasov, 2001, 2005). The absence of modulation of mediated glucose transport in birds may occur because birds rely less on active transport for absorption of glucose and more on passive absorption of glucose.

Microbial Symbionts in Digestion

Cellulose is the most abundant compound in the biosphere and is the primary structural material in plants. However, no vertebrate produces cellulose-digesting enzymes (called cellulases). Digestion of cellulose and other complex carbohydrates in plants by vertebrates is accomplished by microbes (primarily bacteria and some protozoa). The evolution of enlarged portions of the gut to house symbiotic microbes was crucial in the radiation of herbivorous mammals because it provided the appropriate conditions for microbial fermentation to have significant nutritional benefits. Digestion of cellulose is only one of many nutritionally important functions of gut microbes. Microbes ferment dietary carbohydrate and hydrolyse dietary lipids into absorbable nutrients, use nitrogenous compounds including dietary protein to synthesise microbial protein and synthesise vitamins (Van Soest, 1994). **See also**: Coevolution; Mutualistic Symbioses; Vertebrate Herbivory and Its Ecosystem Consequences

Fermentation sites in the gut

Fermentation of plant material occurs in the hindgut and/or foregut of vertebrate herbivores (Stevens and Hume, 1995). Large (>50 kg) hindgut fermenters including horses, rhinos and elephants typically have enlarged colons, whereas small (<10 kg) hindgut fermenters including rabbits, most rodents, some monkeys and most herbivorous birds and reptiles typically have enlarged caeca where plant material is microbially digested. Marsupial herbivores include groups such as the kangaroos and wallabies (Macropodidae), which have their primary site for microbial fermentation in complex, large stomachs, but also include groups such as the wombats (Vombatidae), brushtail possums (Phalangeridae), koala (Phascolarctidae) and gliders (Pseudocheiridae), which have their primary site for microbial fermentation in the hindgut (i.e. colon, caeca or both). **See also**: Digestive System of Amphibians, Reptiles and Birds; Marsupialia (Marsupials); Perissodactyla (Odd-Toed Ungulates Including Horses, Rhinoceroses and Tapirs); Rodentia (Rodents)

Fermentation of plant material in the foregut occurs in enlarged compartment(s) anterior to the true digestive stomach, although these structures are often referred to collectively as a multichambered stomach. Mammals in the suborder Ruminantia (e.g. deer, elk, giraffe, bison, sheep and cattle) and in the order Tylopoda (camels, llama, alpaca and vicuana) have multichambered stomachs. The hoatzin (*Opisthocomus hoatzin*) is the only bird in which portions of the foregut are enlarged and primarily used for fermentation of plant material. **See also**: Artiodactyla (Even-Toed Ungulates Including Sheep and Camels)

Nutritional importance of fermentation and rumination

In vertebrates with multichambered stomachs, fermentation occurs in the first division of the stomach (consisting of the rumen and reticulum in ruminants) and involves the anaerobic conversion of carbohydrates to short-chain fatty acids (SCFAs). SCFAs and amino acids produced by fermentation are absorbed into the bloodstream from the rumen fluid. Partially digested food from the first division of the stomach is regurgitated, chewed and then swallowed and passed into the second division of the stomach (consisting of the omasum and abomasum in ruminants). Hydrolysis and enzymatic digestion of the ruminated food (especially protein in the microbes) occurs in this second division of the stomach. Foregut fermenters that ruminate maximise the breakdown and absorption of nutrients from food because the undigested particles can be regurgitated and remasticated until sufficiently broken down. **See also**: Endosymbionts; Energy Cycle in Vertebrates; Rumen

Foregut fermentation allows the products of fermentation to be efficiently digested and absorbed because the fermentation site is anterior to the intestine where digestion and absorption occurs. SCFAs produced by microbes are the primary source of energy for ruminants (contributing as much as 80% of maintenance energy requirements (Stevens and Hume, 1995)). Digestion of microbial protein provides an important source of amino acids for ruminants. Microbes can synthesise protein from inorganic nitrogen compounds and from urea, a normal waste product of protein metabolism in the liver of herbivores. In many foregut-fermenting animals and especially in ruminants, urea reenters the foregut directly and in part via saliva and is resynthesised into microbial protein. Recycling of urea is especially important for herbivorous animals eating food with low protein. **See also**: Urea Cycle

Foregut fermenters, in general, and ruminants, in particular, are more efficient at utilising dietary nutrients than hindgut fermenters when feeding on moderately fibrous diets because of their ability to maximise digestion of plant material. Foregut fermenters also have an advantage over hindgut fermenters when eating low-protein or low-quality protein foods because they are better able to recycle urea nitrogen and digest microbial protein that usually has all the essential amino acids.

Since fermentation in the hindgut occurs posterior to the primary site of absorption (i.e. the intestine), hydrolysis of microbial protein and absorption of the amino acids is relatively less efficient in hindgut compared to foregut fermenters. Many small hindgut fermenting vertebrates (e.g. rodents, rabbits and hares), however, produce a special kind of faeces from the contents of their caecum and then ingest this faeces (called coprophagy). Coprophagy is nutritionally important because it allows recovery of otherwise lost protein, vitamins and other fermentation products. The nutritional significance of coprophagy is evident when animals are prevented from ingesting caecal faeces. Coprophagic animals that are prevented from ingesting caecal faeces develop vitamin deficiencies (especially vitamin K) and utilise dietary protein and fibre less efficiently.

If primarily high fibre forage is available, then hindgut-fermenting herbivores are favoured over foregut-fermenting herbivores because they can increase their intake and passage rate and so obtain adequate nutrients despite the fast passage rates and large amounts of undigested residue. Foregut-fermenting herbivores have difficulty eating high fibre forage because they selectively retain the large fibre particles in the foregut for so long that the rate of delivery of fermentation products is too slow. If primarily low fibre forage is available, then direct digestion of food is usually more efficient than fermentative digestion. **See also**: Secondary Metabolites: Deterring Herbivores

Diet Diversity and the Evolution of Phenotypic Plasticity

Physiological adaptation can be deduced from comparative studies of physiological traits (e.g. organ size and function, nutrient transport rates and metabolic rate) in vertebrate taxa with different life styles. However, many such physiological traits exhibit considerable variability in ecological time both within and among individuals, which may make it difficult to detect important adapted patterns. The form of phenotypic variation that involves a single genotype producing different phenotypes in response to variation in some environmental variable is called 'phenotypic plasticity'. Rapid reversible changes in organ size and digestive processes provide examples of phenotypic flexibility in that they may flexibly respond to changes in diet. Such phenotypic flexibility in physiological traits may itself be a critical component of the adaptive repertoire of animals that may influence diet diversity, niche width, feeding rate, and thus the acquisition of energy and essential nutrients. **See also**: Biomechanical Studies of Food and Diet Selection; Predator-induced Plasticity

Summary

Vertebrate nutritional ecology focuses primarily on how wild vertebrates procure, digest, absorb and metabolise nutrients in the environment to satisfy their requirements for health, growth and reproduction. A basic understanding of the nutritional ecology of vertebrates is essential for appropriate management of free-living and captive animals. Largely unexplored is the importance of phenotypic plasticity and flexibility in the metabolism, physiology and behaviour of wild animals and how this influences an animal's ability to satisfy its nutritional needs in their natural environment.

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