Nutritional ecology: patterns and processes

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Food is of central importance to everything that an animal does, because it provides energy and the building blocks of the body itself. To explain the ingestion, digestion and absorption of food, the field of nutritional ecology combines various subdisciplines of biology, including morphology, physiology, biochemistry, behaviour and ecology. Several years ago, Karasov and Martinez del Rio (2007) provided a comprehensive examination of how animals process energy, nutrients and toxins. Since then, the field has continued to develop as knowledge is refined by theory and empirical studies. In this Special Issue on nutritional ecology, we contribute further to the field by presenting a collection of articles that each focus on a single topic, but together present a broad overview of current research.

Nutritional ecology starts with the chemistry of food. Protein, carbohydrate and fat vary in their composition and proportion in different foods, and their contributions of amino acids, simple and complex carbohydrates and various fatty acids thus influence the nutritive value of food. Some amino acids and fats must be consumed in the diet because they cannot be synthesised de novo by the body. In addition, food may have a myriad of chemicals and components – such as indigestible material, micronutrients and toxins – that animals must acquire or avoid to meet their nutritional requirements.

Animals forage and select food using sensory systems, such as vision, smell, taste and even touch (for a review of the toughness of food, see Sanson 2006). The taste component may include biting and trituration of food, although species differ in the location of the morphological structures – such as teeth, mandibles, gizzards or proventriculi – involved in these processes. The structure of the digestive system, including the trituration system, may be indicative of the types of food that are processed (Stevens and Hume 1995). Digestive processes include enzymatic digestion and microbial fermentation (Karasov and Martinez del Rio 2007); their locations in the body again vary with taxon and species. The final component of nutrient acquisition is absorption, which includes active transport and diffusion depending upon the type of nutrient (water- or lipid-soluble) and the location where the absorption occurs. These processes of nutrient localisation, acquisition and incorporation have effects on all aspects of animal ecology.

Behavioural, morphological, physiological and biochemical studies of individual species and populations have each contributed different perspectives on diet, food acquisition, digestion and absorption (for a review, see Karasov et al. 2011) that directly influence animal behaviour, populational changes (e.g. birth and death rates) and the nutrient and energy flow through ecosystems. It is an unfortunate consequence of these individual multipronged approaches that it can be easy to get lost in the details and difficult to discern meaningful patterns at the ecological level.

Models of the cost of feeding (Sibly 1981), foraging (Stephens and Krebs 1986), food processing based on chemical reactors (Penry and Jumars 1987), selection for nutrients required (Raubenheimer and Simpson 1994; Simpson and Raubenheimer 1995), and also the use of comparative analyses based on phylogenetically independent contrasts (Felsenstein 1985; Garland Harvey et al. 1992) have improved our understanding of the patterns of foraging, feeding and nutrition among and between taxa. Although the patterns are easier to discern, it is typically individual species or few related species that still form the major focus of research, because of the complexity of working with too many species. However, such studies should improve hypotheses for future work.

Papers in this Special Issue

The topic of this Special Issue arose from the annual meeting of the Australian and New Zealand Society for Comparative Physiology and Biochemistry that was held in 2010 in Canberra, ACT, Australia. In this collection, the first three review articles help identify patterns by comparing various approaches to understanding animal nutrition. The four original research articles that follow attempt to explain some parameters of feeding and the animal response at the level of morphology, physiology or ecology.

In their perspective, Simpson and Raubenheimer (2012) summarise the Geometric Framework (GF) theory of diet selection and the application of the model to a variety of systems. The GF approach permits an examination of how species adjust their changing nutritional needs to a dynamic environment, and this paper clarifies the processes that are involved when using this model in experimental design for a wide range of taxa. Huibert and Abbott (2012) then present an evolutionary perspective on the importance of essential polyunsaturated fatty acids (PUFA) because of their incorporation into the cell membrane. Plants and bacteria can synthesise PUFA, but animals cannot produce either omega-3 PUFA or omega-6 PUFA, so must obtain these from the diet to use in membrane production. Allardyce and Linton (2012) subsequently examine the process of cellulose digestion, normally part of the indigestible component, using herbivorous land crabs, especially Gecarcinus natalis, as model organisms.
They review what is known about the breakdown of cellulose and hemicellulose and discuss the importance of the chelae, mandibles and foregut as sites of mechanical disruption of the plant material, followed by various enzymatic steps to completely digest these compounds.

Andrews et al. (2012) suggest that egg size of phylloxera (Hemiptera: Phylloxeridae) and the number of eggs produced could affect morphology of the digestive system and the subsequent feeding pattern during egg development. Feeding disruptions would occur as eggs developed, so the digestive system has developed to store ingesta during egg production, making the insects capable of surviving for periods without feeding.

Lapidge and Munn (2012) report on the use of doubly labelled water to examine the success of recolonisation of yellow-footed rock wallabies (Petrogale xanthopus celeris) into the wild following captive breeding. They found that water turnover rates changed with water availability, but not with age of pouch young, and that all animals appeared to maintain body condition despite being introduced into new surroundings. Their results suggest that this species can adjust to new conditions of water and food availability successfully.

Pollen can be a protein resource for many birds, but does the way that pollen is preserved before feeding studies affect the ability of birds to digest pollen? Fleming and Moore (2012) studied the ability of New Holland honeyeaters (Phylidonyris novaehollandiae) to access the nutrients within pollen following four pollen storage methods to see if variation observed in previous studies on the importance of pollen in the diet could be explained by storage techniques. Their work indicates that the storage process is less important than the gut transit time among birds, so that individual responses may be more important.

How much energy is needed to process food in crocodilians? Specific dynamic action (the increase in metabolic rate following feeding) can be extremely high in some reptiles, especially snakes (Secor 2009), but does this apply to crocodiles as well? Gienger et al. (2012) examined this question in Crocodylus porosus and C. johnstoni. Metabolic rates are elevated within 24 h to around twice the standard metabolic rate and remain high over 3–4 days in both species. One interesting aspect of their work is that the standard metabolic rate of young C. porosus is higher than that of the adults.

Research on individual species helps shape the models that are derived and these models, in turn, help further explain patterns that are present across taxa. The papers presented in this Special Issue permit further cross-fertilisation between these research components and give insights where further work is required.

**Australian contribution to nutritional ecology**

Australian researchers have contributed significantly to the study of nutritional ecology, although at the time of their work, it may not have been recognised as such; researchers were simply interested in what animals ate and how food influenced their distribution and reproduction.

In entomology, the works of Doug Waterhouse (Waterhouse 1957), Max Day (Day and Grace 1959), Lindsay Barton Browne (Browne 1975), Cliff Ohmart (Ohmart and Edwards 1991) and Michael Slaytor (Slaytor and Chappell 1994) were instrumental in developing an awareness of insect feeding and their requirements for nutrition. Peter Greenaway stimulated much of the work on the digestive changes as crustaceans moved into the terrestrial environment (Greenaway 1994; Greenaway and Linton 1995). Reptile and mammal physiological ecology involved an examination of the range of nutrients (mostly energy and water) required by species across Australia, with both Brian Green (Green 1972; Green 1978; Green and Eberhard 1979) and S. D. Bradshaw (Bradshaw et al. 1994) using doubly labelled water to study animals that are active in the field. Ken Richardson and Ron Wooller described the bill structure and gastrointestinal tracts of several species of birds in relation to their diet (Richardson and Wooller 1986; Richardson and Wooller 1988), while Harry Recher (Recher and Davis 1997; Recher and Davis 1998), Hugh Ford (Ford 1990), and Duke Paton (Paton 1980; Paton and Collins 1989) determined the importance of different food types in the success of wild birds. Ian Hume examined a range of digestive systems and nutrient requirements to generate a picture of the evolutionary changes in digestive systems of marsupials (Hume 1999; Stevens and Hume 1995).

Most of the nutritional ecology research on large animals has benefited from the theories and experiments that emerged from several nutrition studies on stock animals, especially sheep and chickens, that were conducted in the laboratories of agricultural scientists such as David Farrell and Rob Cumming (Balnave et al. 1978; Johnson et al. 1985) and that explored the meat and egg production of animals under various nutrient regimes.

Australia has provided several excellent scientists who have made significant contributions to the emergence of nutritional ecology as a discipline. We dedicate this Special Issue to those researchers who provided the framework for subsequent research in this area.

**References**


