CSIRO PUBLISHING

Australian Journal of Zoology, 2011, **59**, 347–349
http://dx.doi.org/10.1071/ZOv59n6_IN

Introduction

Nutritional ecology: patterns and processes

Paul Cooper

Research School of Biology, Australian National University, Acton, ACT 0200, Australia.
Email: paul.cooper@anu.edu

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. Hulbert 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 celeries*) 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) examine 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

Allardyce, B. J., and Linton, S. M. (2012). Characterisation of cellulose and hemicellulose digestion in land crabs with special reference to *Gecarcoidea natalis*. *Australian Journal of Zoology* **59**, 380–391. doi:10.1071/ZO11054

Andrews, K. B., Kemper, D., Powell, K. S., and Cooper, P. D. (2012). Spatial trade-offs in the digestive and reproductive systems of grape phylloxera. *Australian Journal of Zoology* **59**, 392–399. doi:10.1071/ZO11053

Balnave, D., Farrell, D. J., and Cumming, R. B. (1978). Minimum metabolizable energy requirement of laying hens. *World's Poultry Science Journal* **34**, 149–154. doi:10.1079/WPS19960035

Bradshaw, S. D., Morris, K. D., Dickman, C. R., Withers, P. C., and Murphy, D. (1994). Field metabolism and turnover in the golden bandicoot (*Isoodon auratus*) and other small mammals from Barrow Island, Western Australia. *Australian Journal of Zoology* **42**, 29–41. doi:10.1071/ZO9940029

Browne, L. B. (1975). Regulatory mechanisms in insect feeding. In 'Advances in Insect Physiology. Vol. 11'. (Eds J. E. Treherne, M. Berridge and V. Wigglesworth.) pp. 1–116. (Academic Press: Maryland Heights, MO)

Day, M. F., and Grace, T. D. C. (1959). Culture of insect tissues. *Annual Review of Entomology* **4**, 17–38. doi:10.1146/annurev.en.04.010159.000313

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist* **125**, 1–15. doi:10.1086/284325

Fleming, P. A., and Moore, T. L. (2012). Do experimental methods affect estimates of pollen digestion by birds? *Australian Journal of Zoology* **59**, 407–415. doi:10.1071/ZO12016

Ford, H. A. (1990). Relationships between distribution, abundance and foraging specialization in Australian landbirds. *Ornis Scandinavica* **21**, 133–138. doi:10.2307/3676809

Garland, T. J., Harvey, P. H., and Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**, 18–32. doi:10.1093/sysbio/41.1.4

Gienger, C. M., Tracy, C. R., Brien, M. L., Manolis, S. C., Webb, G. J. W., Seymour, R. S., and Christian, K. A. (2012). Energetic costs of digestion in Australian crocodiles. *Australian Journal of Zoology* **59**, 416–421. doi:10.1071/ZO12018

Green, B. (1972). Water losses of sand goanna (*Varanus gouldii*) in its natural environments. *Ecology* **53**, 452–457. doi:10.2307/1934232

Green, B. (1978). Estimation of food consumption in dingo, *Canis familiaris dingo*, by means of ^{22}Na turnover. *Ecology* **59**, 207–210. doi:10.2307/1936363

Green, B., and Eberhard, I. (1979). Energy requirements and sodium and water turnovers in two captive marsupial carnivores – the Tasmanian devil, *Sarcophilus harrisii*, and the native cat, *Dasyurus viverrinus*. *Australian Journal of Zoology* **27**, 1–8. doi:10.1071/ZO9790001

Greenaway, P. (1994). Salt and water balance in field populations of the terrestrial crab *Gecarcoidea natalis. Journal of Crustacean Biology* **14**, 438–453. doi:10.2307/1548991

Greenaway, P., and Linton, S. M. (1995). Dietary assimilation and food retention time in the herbivorous terrestrial crab *Gecarcoidea natalis. Physiological Zoology* **68**, 1006–1028. doi: www.jstor.org/stable/30163791

Hulbert, A. J., and Abbott, S. K. (2012). Nutritional ecology of essential fatty acids: an evolutionary perspective. *Australian Journal of Zoology* **59**, 369–379. doi:10.1071/ZO11064

Hume, I. D. (1999). 'Marsupial Nutrition.' (Cambridge University Press: Cambridge.) 434 pp.

Johnson, R. J., Cumming, R. B., and Farrell, D. J. (1985). Influence of food restriction during rearing on the body-composition of layer-strain pullets and hens. *British Poultry Science* **26**, 335–348. doi:10.1080/00071668508416821

Karasov, W. H., and Martinez del Rio, C. (2007). 'Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins.' (Princeton University Press: Princeton, NJ.) 741 pp.

Karasov, W. H., Martinez del Rio, C., and Caviedes-Vidal, E. (2011). Ecological physiology of diet and digestive systems. *Annual Review of Physiology* **73**, 69–93. doi:10.1146/annurev-physiol-012110-142152

Lapidge, S. J., and Munn, A. J. (2012). Seasonal field metabolic rate and water influx of captive-bred reintroduced yellow-footed rock-wallabies (*Petrogale xanthopus celeris*). *Australian Journal of Zoology* **59**, 400–406. doi:10.1071/ZO11049

Ohmart, C. P., and Edwards, P. B. (1991). Insect herbivory on *Eucalyptus. Annual Review of Entomology* **36**, 637–657. doi:10.1146/annurev.en.36.010191.003225

Paton, D. C. (1980). The importance of manna, honeydew and lerp in the diets of honeyeaters. *Emu* **80**, 213–226. doi:10.1071/MU9800213

Paton, D., and Collins, B. (1989). Bills and tongues of nectar-feeding birds: a review of morphology, function and performance, with intercontinental comparisons. *Australian Journal of Ecology* **14**, 473–506. doi:10.1111/j.1442-9993.1989.tb01457.x

Penry, D. L., and Jumars, P. A. (1987). Modeling animal guts as chemical reactors. *American Naturalist* **129**, 69–96. doi:10.1086/284623

Raubenheimer, D., and Simpson, S. J. (1994). The analysis of nutrient budgets. *Functional Ecology* **8**, 783–791. doi:10.2307/2390238

Recher, H. F., and Davis, W. E. (1997). Foraging ecology of a mulga bird community. *Wildlife Research* **24**, 27–43. doi:10.1071/WR96052

Recher, H. F., and Davis, W. E. (1998). The foraging profile of a wandoo woodland avifauna in early spring. *Australian Journal of Ecology* **23**, 514–527. doi:10.1111/j.1442-9993.1998.tb00762.x

Richardson, K. C., and Wooller, R. D. (1986). The structures of the gastrointestinal tracts of honeyeaters and other small birds in relation to their diets. *Australian Journal of Zoology* **34**, 119–124. doi:10.1071/ZO9860119

Richardson, K. C., and Wooller, R. D. (1988). The alimentary-tract of a specialist frugivore, the mistletoebird, *Dicaeum hirudinaceum*, in relation to its diet. *Australian Journal of Zoology* **36**, 373–382. doi:10.1071/ZO9880373

Sanson, G. (2006). The biomechanics of browsing and grazing. *American Journal of Botany* **93**, 1531–1545. doi:10.3732/ajb.93.10.1531

Secor, S. M. (2009). Specific dynamic action: a review of the postprandial metabolic response. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **179**, 1–56. doi:10.1007/s00360-008-0283-7

Sibly, R. (1981). Strategies of digestion and defecation. In 'Physiological Ecology: An Evolutionary Approach to Resource Use'. (Eds C. R. Townsend and P. Calow.) pp. 109–139. (Blackwell Scientific Publications: Oxford.)

Simpson, S. J., and Raubenheimer, D. (1995). The geometric analysis of feeding and nutrition – a users guide. *Journal of Insect Physiology* **41**, 545–553. doi:10.1016/0022-1910(95)00006-G

Simpson, S. J., and Raubenheimer, D (2012). The nature of nutrition: a unifying framework. *Australian Journal of Zoology* **59**, 350–368. doi:10.1071/ZO11068

Slaytor, M., and Chappell, D. J. (1994). Nitrogen metabolism in termites. *Comparative Biochemistry and Physiology. Part B, Biochemistry & Molecular Biology* **107**, 1–10. doi:10.1016/0305-0491(94)90218-6

Stephens, D. W., and Krebs, J. R. (1986). 'Foraging Theory.' (Princeton University Press: Princeton, NJ.) 247 pp.

Stevens, C. E., and Hume, I. D. (1995). 'Comparative Physiology of the Vertebrate Digestive System.' 2nd edn. (Cambridge University Press: Cambridge.) 400 pp.

Waterhouse, D. F. (1957). Digestion in insects. *Annual Review of Entomology* **2**, 1–18. doi:10.1146/annurev.en.02.010157.000245