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Patterns and processes in the vertebrate digestive system

In his famous treaty on biological diversity, G.E. Hutchinson[1] noted that 'In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously more to living communities than the raw dictum "eat or be eaten" but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.' Accordingly, studies of food relations and the underlying dynamic flow of energy and nutrients between organisms have been centrally important for our understanding of ecology at the individual, population, community and ecosystem levels and for our understanding of the evolution of ecological systems.

Another important raw dictum 'we are what we do not defecate' reminds us, however, that organisms do not assimilate all the available resources in their food. This inefficiency can result from apparent phylogenetic constraints (e.g. passerines in the Sturnidae–Muscicapidae taxon lacking the enzyme to digest sucrose[2]) or from compounds in the food (e.g. fiber or toxins in plants) that retard or inhibit the breakdown and absorption of ingested nutrients. In April, a group of comparative physiologists and anatomists from across the globe gathered in Rauischholzhausen, Germany, to discuss recent advances in the study of the vertebrate digestive system and their ecological and evolutionary implications. The workshop, organized and hosted by P. Langer and R. Snipes (both of Justus-Liebig-Universitat, Giessen, Germany), and J.M. Starck (Universität Tübingen, Germany), was a sequel to one held five years earlier in Cambridge, UK, which focused on the theme of food, form and function in the digestive system of mammals[3]. Both workshops promoted interdisciplinary investigations into the patterns and processes of the digestive system; however, the most recent workshop was expanded to include interdisciplinary research on mammals, birds and reptiles.

Three contemporary themes in the study of the vertebrate digestive system were explored: comparative anatomy and the evolution of the digestive system, form and function of the digestive system in relation to dietary niche and nutrition, and ecological and evolutionary implications of phenotypic plasticity in the digestive system.

The first step in the analysis of any biological system is often the description of morphology and its apparent function, and the workshop included exciting presentations about the digestive system of vertebrate groups for which very little is known. N. Zhukova (Institute of Zoology, Kiev, Ukraine) used characters of the digestive system to suggest a close phylogenetic relationship between the Insectivora (e.g. moles, shrews, hedgehogs), Chiroptera (bats), and certain lower primates (the Tupaiidae). M. Olsen and S. Mathiesen (University Tromso, Norway) discussed the functional morphology of the whale's digestive system. Their studies of the forestomach of bowhead, grey, fin and minke whales revealed remarkable functional similarities to the rumen of ruminants: slightly acidic pH (5.3–6.8), high concentrations of anaerobic bacteria (some can digest the chitinous exoskeleton of their invertebrate prey) and the presence of volatile fatty acids.

Complementing the presentations on the digestive system of less studied vertebrates were two very informative reviews of large-scale patterns in gut form and function. R. Snipes, H. Hornicke and G. Bjornhag (Swedish University of Agricultural Sciences, Uppsala, Sweden), presented an exhaustive review of the

  0169-5347/97/$17.00 PII: S0169-5347(97)01201-9

intestinal anatomy of mammals in relation to dietary habits. Langer reviewed the morphology of the digestive tract in relation to postnatal life history in eutherian (placental) mammals. He showed that the weaning period tended to be long in eutherian mammals such as ruminants that digest cellulose, presumably because these young mammals need time to establish a well-balanced microbial flora. However, weaning period was also long in many eutherians without fermentation of cellulose, suggesting a complex interplay between the evolution of such life history features and the morphology of the digestive tract.

Animals vary little in the nutritional resources they offer to potential consumers. In contrast, the widely different nutritional resources provided by plants and their parts have led herbivores to face many problems of digestion not encountered by carnivores. Current work on how vertebrate frugivores and folivores solve the problems of digesting their respective plant food was prominent at the workshop.

Typically, fruits provide consumers with lots of energy, large amounts of non-nutritive material (e.g. pulp fiber, skin, indigestible seeds), and little protein. The hypothesis that fruit characteristics related to seed dispersal have coevolved with certain sensory adaptations of their consumers gained little support from J.U. Ganzhorn's (Deutsches Primatenzentrum, Göttingen, Germany) research with primates. M. Witmer (University of Wyoming, Laramie, USA) argued that specializations in intestinal morphology of fruit-eating waxwings and thrushes may facilitate high intake of fruit and rapid passage rates, but the rapid passage of digesta may impair the utilization of lipids in fruit. F. Bairlein (Institute fuer Vogelforschung, Wilhelmshaven, Germany) discussed the nutritional adequacy of fruits for songbirds that feed on fruits during migratory periods when nutritional demands are high. He found that the ability of migratory warblers to maintain and accumulate body mass on fruit-only diets depends on an adequate acclimation time and the type of fruit.

Current work on the digestive system of folivores was well represented at the meeting. O. Timoshenko (Institute of Zoology, Kiev, Ukraine) provided a synopsis of the diversity, hosts and evolution of hindgut ciliates in folivorous mammals. M. Wikelski (University of Washington, Seattle, USA) demonstrated that environmental temperature and food supply directly influenced body size of algae-eating marine iguanas (*Ambylyrhyncus cristatus*) via constraints on food intake and digestion. M.G. Dominguez-Bello (Laboratorio de Fisiología Gastrointestinal, Caracas, Venezuela) reviewed the digestive physiology of the hoatzin (*Opisthocomus hoatzin*), the only known foregut fermenting bird. Contrary to earlier reports, she found that the bacteria and protozoa within the hoatzin's enlarged crop had low cellulolytic activity. This raised the question whether microbes within the hoatzin's crop primarily degrade non-cellulose fiber as in other avian herbivores or degrade cellulose as in other foregut fermenters such as ruminants.

A major theme in the study of the nutritional ecology of herbivores has been the constraints imposed by body size on the use of fiberous diets[4]. S. Cork (Division of Wildlife and Ecology, CSIRO, Australia) and W. Karasov (University of Wisconsin, Madison, USA) used a modeling approach to investigate interactions between body size, dietary fiber, and digestive and foraging strategies in vertebrate herbivores. Their model predicted allometric constraints on the fermentative use of fiberous diets but showed that gut expansion and selective retention of more digestible components of the diet could largely alleviate such constraints. Recent empirical work (S. McWilliams and W. Karasov) on small avian herbivores (e.g. geese and grouse) provides support for the model's predictions and also suggests that modulation of nutrient uptake rates can be important for easing proposed allometric constraints.

The important question of how plant secondary metabolites (PSMs) might effect food intake and selection in mammalian herbivores was reviewed by W. Foley (Australian National University, Canberra, Australia) and C. McArthur (University of Tasmania, Australia). They argued that answering such a question is complicated because, at least for browsing marsupials, the mechanism(s) for detecting and regulating food intake depended on the type of PSMs present.

One encompassing theme of the meeting was the occurrence and functional significance of phenotypic plasticity of the digestive system[5]. For the functional anatomist interested in the evolution of the digestive system, phenotypic plasticity can be a major nuisance because it may obscure important adapted patterns. For the ecologist or comparative physiologist, however, such plasticity offers opportunities to study how the digestive system may permit or constrain the response of animals to environmental and ontogenetic change.

T. Sakata (Ishinomaki Senshu University, Ishinomaki, Japan) demonstrated that the growth rate of the intestine of young rats changed just before weaning, suggesting that the intestine does not adapt to the nutritional changes at weaning, but instead anticipates this nutritional shift. S. Secor and J. Diamond (University of California, Los Angeles, USA) found that gut size and function in infrequently feeding snakes (e.g. sit-and-wait foraging pythons) decreased when the snake was not digesting a meal and then dramatically increased when the snake caught a meal. In contrast, the digestive strategy of snakes that feed regularly (e.g. active foraging racers) was similar to most vertebrates: continuously maintain a fully functional gut with more modest abilities to change. J.M. Starck discussed phenotypic plasticity in the morphology of the avian digestive system. In response to increased food intake or lower quality diets, the guts of many birds increase in size and mass because of important changes at the ultrastructural level. Starck emphasized that we currently know little about the time scale of these responses and the processes that regulate the reconstruction of the gut.

W. Karasov reviewed results from recent empirical tests of an optimal digestion model. The model makes specific predictions about how an animal's digestive system should respond to rapid changes in food quality or quantity like those experienced by birds during migration. Because none of the empirical results fit the predictions of the model, Karasov questioned whether birds maximize their rate of energy gain as assumed by the model. He suggested that birds may instead minimize their feeding time by maximizing their extraction efficiency.

C. Martínez del Rio (University of Wyoming, Laramie, USA) reviewed the evidence in birds for modulation of digestive proteins (i.e. intestinal glucose transporters and membrane-bound digestive enzymes such as carbohydrases) in response to diet and in relation to dietary niche. He found little support for the adaptive modulation hypothesis[6], which argues that digestive performance is matched to the prevailing diet and is modulated with changes in diet quality or quantity. D. Afik (University of Haifa, Oranim, Israel) presented evidence that the digestive system of an omnivorous warbler (*Dendroica coronata*) both permits and constrains the response of an animal to dietary change and ultimately to its dietary niche. For example, by modulating retention time, warblers maintained relatively high digestive efficiency despite dramatic shifts in diet (i.e. fruit, insect and seed diets); in contrast, starch digestion was always limited by low enzyme hydrolysis rates. I. Hume (University of Sydney, Australia) and H. Biebach (Max Planck Institute Verhaltensphysiology, Kloster Ansechs, Germany) showed that the digestive tract of migratory garden warblers (*Sylvia borin*) rapidly reduced in size when birds did not feed, as occurs during their migratory flight over the Mediterranean Sea and Sahara Desert. The consequences of this reduction in gut size include decreased food intake, longer retention time, and higher extraction efficiency on the first day following a fast compared to days later when the gut has been rebuilt.

This is an exciting time for scientists interested in the physiology, ecology and evolution of the vertebrate digestive system. New tools are now available that facilitate applying the comparative method for investigating the evolutionary ecology of feeding and digestion while considering phylogeny[7]. Recent new discoveries (e.g. foregut fermentation in birds and whales) and empirical tests of optimal digestion models have inspired careful scrutiny of contemporary theory. And plasticity in many digestive features of birds, reptiles and mammals has proven to be common and to have important implications for ecologists and evolutionary biologists alike.

Acknowledgements
We are grateful to P. Langer, R. Snipes, and J.M. Starck for an excellent workshop. Special thanks to D. Dearing and J.M. Starck for their help during the writing of the manuscript.

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Mitochondrial Eve: the plot thickens

The hypothetical descent of mankind from 'mitochondrial Eve'[1] has been much debated since the first report of Cann *et al.*[2] in 1987. While some claim 800 000 years to be an upper limit[3], most researchers suggest a date of approximately 200 000 years[1,2,4]. Occasionally, even figures as low as 70 000 years are reported[5]. A new paper on mutation rates actually measured in mitochondria now seems to generate further complexity[4].

Nobody was actually there ...

Typical mitochondrial Eve studies usually combine two elements. To get an idea about the period when mitochondrial Eve lived, possibly giving rise to all human mtDNAs observed today, they (1) evaluate mtDNA sequence data and (2) estimate annual substitution rates. Sequences come from mtDNA of populations whose most recent common ancestor is to be determined. Based on their differences phylogenetic trees can be constructed using various methods. A number of sophisticated techniques provide reasonable reliability to this part of most studies, although some uncertainty always remains[1].

To calibrate substitution rates, an outgroup is needed, as well as the time of divergence between that outgroup and the populations studied. The standard approach uses great apes (e.g. *Pan troglodytes*, the chimpanzee) as an outgroup and around five million years as a divergence date, derived from paleontological evidence. Evolutionary substitution rates inferred by this kind of approach range from 0.025 to 0.26 substitutions/site/million years, corresponding to an age of approximately 60 000 to 630 000 years for 'Eve'[4]. Results are based on a correct date of divergence between great apes and humans, which is disputed. Furthermore, a constant substitution rate for all sites investigated and the total period of time elapsed (i.e. a molecular clock) must be postulated. Mitochondrial Eve studies either argue for some kind of neutrality of the sites investigated and, hence, for constant substitution rates, or they aim to quantify deviations from neutrality. In addition, one must assume that the molecular clock ticks with the same rate in apes and humans. Definitive proof is difficult, since none of us was actually there. What is needed, therefore, are experimental data which measure mutation rates directly. This is where Parsons *et al.* come in[4].

Independence Day for mutation rate measurements?

With the advent of powerful methods for accurate sequencing at a large scale, mutation rates can be estimated by comparing sequences of individual parent–child pairs ('generational events'). Based on phylogenetic considerations, Parsons *et al.* expected approximately one mutation in 600 generations[4]. Surprisingly, they detected a roughly 20-fold higher mutation rate of the mtDNA control region used in typical Eve studies. They sequenced 610 basepairs of 357 individuals from 134 independent mtDNA lineages, thus screening 327 generational events, and found 10 substitutions. Excluding sequencing errors, they calculate an intergenerational (roughly 20 years) substitution rate of 1.2–4.0/site/million years (95% confidence interval, 2.5 as mean value), if extrapolated to a large timescale. If molecular evolution is really neutral at these sites, such a high mutation rate would indicate that Eve lived about 6500 years ago – a figure clearly incompatible with current theories on human origins. Even if the last common mitochondrial ancestor is younger than the last common real ancestor, it remains enigmatic how the known distribution of human populations and genes could have arisen in the past few thousand years[4].

Other puzzling observations

Parsons *et al.* are not the only ones suggesting rapid evolution of mitochondria. A year earlier, Howell *et al.*[6] reported two substitutions per 80 (approx.) generational events in the control region of mtDNA, which corresponds to roughly two substitutions/site/million years and is in excellent agreement with the Parsons values, even if based on a smaller sample of generational events. Interestingly, a 200-fold higher intergenerational substitution rate than derived from phylogenetic approaches was found in human mtDNA coding regions[6,7].

Another interesting detail comes from a mitochondrial Eve study in cattle[8,9]. The

  0169-5347/97/$17.00 PII: S0169-5347(97)01204-4