

The gut in feast and famine

Andrew R. Cossins and Neil Roberts

WITH the season of excess just over in many parts of the world, now is as good a time as any to ponder the physiological effects of overeating. The post-prandial slump is one such consequence, as blood is diverted to the intestines and liver, and the rest of the body relaxes to expedite digestion. Two papers by Secor and colleagues^{1,2} show that the demands we might put on the digestive system by eating especially large meals are nothing compared to those experienced by some snake species. These studies provide a new and spectacular model for investigating how the digestive physiology of vertebrates may be adapted to altered functional needs.

several months. But when a meal does arrive it can be of gigantic proportions. It is not unusual for pythons to consume up to 50 per cent of their own body weight at one sitting and there are published accounts of up to 160 per cent⁵. These enormous meals can be digested and assimilated in just a few days. Exactly how the snakes' digestive systems respond to extended periods of fasting followed by massive feeding was unknown.

Secor and colleagues have therefore followed the changes in intestinal structure and function in the Burmese python¹ and sidewinder rattlesnake² during the few days after feeding. They show that the small

gastric hydrochloric acid, and its oxygen partial pressure plunges to a quarter of its normal value, indicating the intensity of aerobic metabolism. Indeed, Secor and Diamond¹ show that whole-animal oxygen consumption of pythons increases 17 times only 24 hours after feeding (that of the rattlesnake increases seven times²). This huge factorial increase is comparable to that shown by sprinting mammals, but pythons maintain the increase for several days while remaining virtually motionless.

Of course, all of this increased activity comes at a considerable energetic cost. Secor and Diamond estimate that some 32 per cent of the metabolizable energy of the food in the python is consumed during the oxidative burst that supports digestion, against 10–23 per cent in animals that feed more-or-less continually. Although this extra energetic cost is attributable to mucosal upregulation, it is more than offset by the energetic savings from not maintaining a functional mucosa during the long period between meals.

These two studies provide an unusually clear picture of the remarkable extent to which physiology can respond to the fluctuating demands imposed by unusual lifestyles. They also open up some new research options in the study of gastrointestinal function. First, in contrast to virtually all other vertebrates, the digestive system of snakes is linear from mouth to anus⁶, and this morphological simplicity facilitates analysis. Second, the size of large snakes such as the Burmese python makes them convenient for study by whole-body magnetic resonance imaging (MRI). Conventional MRI can monitor gastric emptying and peristaltic movements⁷; high-resolution MRI techniques can characterize and monitor the response of the intestinal mucosa; and MR spectroscopy with phosphorus-31 offers the prospect of directly and non-invasively investigating metabolic processes in a snake's internal organs and tissues, including quantification of pH changes during digestion. It is a fair bet that many of the gastrointestinal processes in snakes are evident in other animals, albeit in less extreme form. □

Gunter Ziesler/Bruce Coleman

IMAGE
UNAVAILABLE
FOR COPYRIGHT
REASONS

Tough act to swallow — a rock python makes a meal of a Thomson's gazelle.

Digestion and assimilation consume a considerable fraction of the energy made available in the food itself. This energy is required not only to power digestion, absorption and the processing of food, but also for the maintenance of the digestive structures themselves. The mucosal lining of the vertebrate small intestine is a morphologically complex tissue with a very active metabolism. This, together with the remarkably high rate of cell loss and renewal, make it an energetically expensive tissue to maintain in prime condition³, and animals that are periodically under severe energetic constraints may not be able to sustain the cost. An example is that of ground squirrels, which undergo a noticeable reduction in mucosal thickness during hibernation⁴; hibernation is a strategy for energy saving and part of the strategy is to shut down expenditure on maintenance of the intestine.

A second case is that provided by those bradymetabolic animals (that is, having a low energy consumption) that feed intermittently. The most extreme examples are the vipers, boa constrictors and pythons, which, being sit-and-wait predators, eat infrequently, their meals often being separated by long and unpredictable fasts of

intestine of fasting individuals has an atrophied mucosal lining. Feeding, however, initiates a period of rapid reconstruction and the weight of the small intestine in both species doubles within a few hours entirely due to an increase in mucosal thickness. This massive reconstruction project occurs well before any assimilation of the meal can occur and the costs therefore must be met by committing energy reserves well before any payback.

Measurements of nutrient absorption in isolated intestinal preparations show that the functional capacity of the system increases far more than expected from the doubling of the mucosal weight. Thus uptake rates for radiolabelled amino acids at the mucosal brush border in pythons increased by six times after 24 hours and by 16 times after three days, probably because of an increased capacity of the underlying transport systems combined with a doubling (or more) of mucosal surface area. Interestingly, in pythons these upregulated intestinal activities greatly exceed those of another bradymetabolic, continuously feeding carnivore (rainbow trout) and bear comparison with those of mammalian carnivores. The blood shows a strong alkalosis, probably due to the intense production of

Andrew R. Cossins is in the Department of Environmental and Evolutionary Biology, and Neil Roberts is in the Magnetic Resonance Centre, University of Liverpool, Liverpool L69 3BX, UK.

1. Secor, S. M. & Diamond, J. *J. exp. Biol.* **198**, 1313–1325 (1995).
2. Secor, S. M. & Nagy, K. A. *Ecology* **75**, 1600–1614 (1994).
3. Johnson, L. R. in *Physiology of the Gastrointestinal Tract* (ed. Johnson, J. R. Jr) 301–333 (Raven, New York, 1987).
4. Carey, H. V. & Sills, N. S. *Am. J. Physiol.* **263**, R517–R523 (1992).
5. Green, I. I. W. in *Biology of Pit Vipers* (eds Campbell, J. A. & Brodie, E. D. Jr) 107–111 (Selva, Tyler, Texas, 1992).
6. Parker, H. W. & Grandison, A. G. C. *Snakes—A Natural History* 2nd edn (British Museum of Natural History/Cornell Univ. Press, 1977).
7. Stehling, M. K. *et al. Radiology* **171**, 41–46 (1989).