

**THE NUTRITION, DIGESTIVE PHYSIOLOGY AND
METABOLISM OF POTOROINE MARSUPIALS**

A thesis submitted to

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by

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TO ... Streetfighter, Rufous and the Archbishop

. . . . three flamboyant potoroine marsupials.

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PREFACE

The studies presented in this thesis were completed by the author while a part-time student in the Department of Biochemistry, Microbiology and Nutrition, University of New England, Armidale, NSW, Australia. Assistance given by other persons is indicated in the text or in the list of acknowledgements. All references cited are included in the bibliography. The work is otherwise original.

* * *

I certify that the substance of this thesis has not already been submitted for any degree and is not being currently submitted for any other degree. I certify that any help received in preparing this thesis, and all sources used have been acknowledged in the thesis.

August 1990

I R Wallis

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ABSTRACT

The nutrition, digestive physiology and metabolism of potoroine marsupials

THE nutrition, digestive physiology and metabolism of potoroine marsupials, the smallest macropodoids, was studied in one species from each of the extant genera. Those studied, all of which were captive, included *Aepyprymnus rufescens* (rufous rat-kangaroo), *Potorous tridactylus* (long-nosed potoroo) and *Bettongia penicillata* (brush-tailed bettong). Although several studies have been made of different aspects of potoroine marsupials, this is the first pertaining to an integrated study of their nutrition, metabolism and digestive physiology. It was, therefore, a general study. Its primary aim was to provide a platform for future research on more specific subjects.

A discussion of herbivory, with particular emphasis on body size and gastrointestinal function, suggested that potoroine marsupials are concentrate-selecting herbivores. This thesis is supported by the few studies of potoroine feeding ecology, which have identified hypogeous fungi, roots, tubers, seeds, gum and invertebrates as important food items. Thus, a standard diet composed mainly of cereals supplemented with oaten chaff was developed for maintenance of the animals. Potoroines selected this diet in preference to a lower energy lucerne-based formulation.

Most experiments were conducted with maize-oat hull diets that contained about 1% nitrogen. This was enough to maintain positive nitrogen balance in animals with average food intakes. These nitrogen requirements were determined with *A. rufescens* fed diets containing three levels of nitrogen and two levels of plant-cell walls. Nitrogen balance was not affected by the level of dietary fibre. Consequently, the data were pooled to give a truly digestible nitrogen requirement of $200 \text{ mg.kg}^{-0.75}.\text{d}^{-1}$ for animals fed diets with neutral-detergent fibre levels between 100 and 300 g per kg dry matter. Nitrogen balance data from other experiments indicated that *P. tridactylus* and *B. penicillata* have nitrogen requirements similar to those of *A. rufescens*. A comparison of the present results with those published for eutherian and other metatherian species showed that, as expected, the nitrogen requirements of potoroine marsupials are markedly less than those of most eutherians. Less expected was the finding that the maintenance nitrogen requirements of potoroine marsupials are similar to those of some arid-zone macropodids, such as *Macropus robustus erubescens* (euro).

The relationships between the various urea kinetic parameters suggested that urea metabolism in potoroine marsupials is similar to that reported in other species. Because the studies were conducted using diets that later proved detrimental to microbial metabolism, it was concluded that urea recycling was probably of little nutritional value. Thus, the low nitrogen requirements of potoroine marsupials reported in Chapter 5 are not necessarily linked to urea metabolism.

No differences in the kinetics of urea metabolism were found between *A. rufescens* fed lucerne-based diets with differing levels of cereal. This was not surprising because cellulolytic activity, as indicated by cell-wall digestibility, was similar in the two diets.

Severe water restriction significantly increased all urea kinetic parameters — for example, the rates of synthesis and degradation. This reflects the link between urea conservation and water conservation. In potoroine marsupials with high levels of microbial metabolism, urea recycling is probably important for providing a continuous supply of nitrogen to the gut, so that digestion continues during the resting phase.

The passage of digesta through the potoroine gut was investigated with the dual marker system of ^{103}Ru -Phenanthroline, which marks the particulate matter, and ^{51}Cr -EDTA, a solute marker. The similar mean retention times (MRT) (ca 25-30 hours) of ^{103}Ru -P and ^{51}Cr -EDTA in the gastrointestinal tracts of potoroine marsupials contrasts with the marked separation of digesta phases in macropodids. The different patterns of digesta flow, in the two groups, were explained by differences in foregut anatomy. No significant differences were found between *A. rufescens*, *P. tridactylus* or *B. penicillata* for any parameter of digesta passage. Because MRT were often between 24 and 30 hours, it was suggested that the nocturnal habit of potoroine marsupials might be an important regulator of digesta flow. Digesta passage was not affected by the level of dietary plant-cell wall constituents, or the level of gut fill when the markers were administered. It is suggested that future studies examine the effects of particle size, the transit of low-concentrate diets and the possibility that, although solutes and particles have similar MRT, they flow through the gut independently.

A series of three experiments was conducted to investigate the relationships between digestibility, the source of dietary plant-cell-wall constituents and the ratio of grain to plant-cell-wall constituents in potoroine diets. Poroine marsupials digested a small proportion only (10-20%) of the structural carbohydrates in diets containing maize and up to 50% oat hulls. Furthermore, this digestion was associated with much variation, both within- and between-animals. Poroines ate more in response to the nutrient-diluting effect of the oat hulls, but this did not affect NDF digestibility. In contrast to their performance on the maize-oat hull diets, poroines digested 60% of the NDF in a lucerne-based diet containing 50% NDF. However, the digestibility of NDF

in a less fibrous (33% NDF) lucerne-based diet was only 30%. It was concluded that the foregut environment of potoroine marsupials is extremely labile and that cellulolysis is related inversely to the level of soluble carbohydrates in the diet. The inhibition of cellulolysis by soluble carbohydrates was confirmed by low pH (4.3), low short-chain fatty-acid concentrations, and low *in vitro* production rates of short-chain fatty-acids in forestomach digesta taken from *A. rufescens* and *P. tridactylus* fed cereal-based diets. By comparison, the values for these parameters in free-living *A. rufescens* were similar to those reported in the literature for several foregut- and hindgut-fermenting herbivores.

Water consumption was measured in all experiments. Also, flux was measured in *A. rufescens*, *P. tridactylus* and *B. penicillata* housed in outdoor enclosures, and in free-living *A. rufescens*. Potoroine marsupials drank more water when the levels of nitrogen and cell-wall constituents in maize-oat hull diets were increased. However, potoroines drank most water when fed lucerne-based diets. When measurements were made in metabolism cages, *P. tridactylus* consistently drank more water per unit metabolic body mass than did *B. penicillata* or *A. rufescens*. The smaller species had higher evaporative water losses — attributed to their higher activity. In the outdoor enclosures the water-turnover rates were similar between species and seasons. All three species, when dehydrated, tolerated losses of body mass of about 20%. Under these conditions, their constant PCV, their ability to concentrate urine and produce dry faeces, and their ability to rehydrate rapidly, all suggest some drought tolerance. Lactating animals, captive or wild, did not drink more than non-lactating animals. Free-living *A. rufescens* had similar WTR in summer and winter. However WTR increased during periods of rain.

Daytime and night-time measurements of fasting heat production were made on *A. rufescens*, *P. tridactylus* and *B. penicillata* starved for 6-54 hours. RQ was similar in all species (0.75-0.80). The night-time activity of *P. tridactylus* and *B. penicillata* doubled their FHP; that of *A. rufescens* was increased by only 25%. Starvation reduced RQ but did not affect heat production. The minimum mean FHP for each species was 11-20% lower than the mean value for eutherians.

The maintenance requirement for *A. rufescens* ($340 \text{ kJ.kg}^{-0.75}.\text{d}^{-1}$) was about 25% lower than values reported normally for eutherian stock. The corresponding maintenance requirements for *P. tridactylus* and *B. penicillata* were similar to the energy needs of eutherians. The differences between potoroine species were again explained by the higher activity of the smaller species.

The energy expenditure by female *A. rufescens* was measured before lactation and at specific times during the development of pouch young. Simultaneous analyses of milk composition were made also. In the week preceding pouch vacation, the combined

heat production of the female *A. rufescens* and her young were about 20% higher than that of the barren female. The changes in milk composition were similar to those reported in other metatherians. It was concluded that the long lactation of *A. rufescens* serves to minimize nutrient output at any one time. Therefore, the lactational strategy is ideally suited to an unpredictable environment.

The metabolic rate of free-living *A. rufescens* was found to be $650 \text{ kJ.kg}^{-0.75}.\text{d}^{-1}$ or 2.9 times the lowest metabolic rate of fasting animals determined in Section 11.1. The FMR was similar in winter and summer even though the difference in mean minimum temperatures between the two seasons was 20°C . The DLW method did not detect any differences in FMR between males and females. A poor understanding of the diet and the behavioural ecology of *Aepyprymnus* makes it difficult to explain the similarities between sexes and seasons.

The present study found very few differences in digestive physiology or metabolism between *A. rufescens*, *P. tridactylus* or *B. penicillata*. It was concluded that potoroine marsupials are extremely flexible. Although there are few potoroine species and their variety has changed little since the Miocene era, the diversity of the group, as indicated by the different habitats they once occupied, is remarkable.

Unfortunately, in view of the fact that Australia has one of the highest mammalian extinction-rates in recent times, and that its unique fauna still holds a very low profile, the future of free-living potoroine marsupials is very limited.

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Scientific Names

In this thesis many mammals are mentioned that might have scientific names that are unfamiliar to the reader. Therefore, the english common name is given when the mammal is first mentioned but, thereafter, the scientific name only is used. Domesticated species — for example, sheep, cow, goat — are referred to by their common names only. The following table gives a complete list of scientific and common names used in the thesis. For ease of reference they are listed alphabetically within their classes or sub-classes. The terms *metatherian* and *marsupial* are used interchangeably throughout the thesis.

Table P1 Scientific and common names of mammals used in this thesis

Scientific name	Common name
Metatherians	
<i>Aepyprymnus rufescens</i>	rufous rat-kangaroo
<i>Antechinus swainsonii</i>	dusky antechinus
<i>Bettongia gaimardi</i>	Tasmanian bettong
<i>Bettongia leseur</i>	burrowing bettong
<i>Bettongia penicillata</i>	brush-tailed bettong
<i>Bettongia tropica</i>	Queensland bettong
<i>Caloprymnus campestris</i>	desert rat-kangaroo
<i>Dasyercus cristicauda</i>	mulgara
<i>Dasyuroides byrnei</i>	kowari
<i>Dasyurus maculatus</i>	spotted-tailed quoll
<i>Dasyurus viverrinus</i>	eastern quoll
<i>Gymnobelideus leadbeateri</i>	Leadbeater's possum
<i>Hypsiprymnodon moschatus</i>	musky rat-kangaroo
<i>Isodon macrourus</i>	northern brown bandicoot
<i>Lagorchestes spp</i>	hare-wallabies
<i>Macropus agilis</i>	agile wallaby
<i>Macropus eugenii</i>	tammar wallaby
<i>Macropus fuliginosus</i>	western grey kangaroo
<i>Macropus giganteus</i>	eastern grey kangaroo
<i>Macropus parma</i>	parma wallaby
<i>Macropus robustus erubescens</i>	euro
<i>Macropus robustus robustus</i>	eastern wallaroo
<i>Macropus rufogriseus</i>	red-necked wallaby
<i>Macropus rufus</i>	red kangaroo
<i>Macrotis lagotis</i>	bilby
<i>Notomys spp</i>	hopping mice
<i>Odocoileus virginianus</i>	Virginian opossum
<i>Onychogalea spp</i>	nailtail wallabies
<i>Perameles nasuta</i>	long-nosed bandicoot
<i>Petauroides volans</i>	greater glider
<i>Petaurus breviceps</i>	sugar glider
<i>Petrogale concinna</i>	nabarlek
<i>Petrogale inornata</i>	unadorned rock-wallaby
<i>Petrogale lateralis</i>	black-footed rock-wallaby
<i>Phascolarctos cinereus</i>	koala
<i>Potorous longipes</i>	long-footed potoroo
<i>Potorous platyops</i>	broad-faced potoroo

<i>Potorous tridactylus</i>	long-nosed potoroo
<i>Pseudocheirus peregrinus</i>	common ringtail possum
<i>Sarcophilus harrisi</i>	Tasmanian devil
<i>Setonix brachyurus</i>	quokka
<i>Sminthopsis crassicaudata</i>	fat-tailed dunnart
<i>Thylogale stigmatica</i>	red-legged pademelon
<i>Thylogale thetis</i>	red-necked pademelon
<i>Vombatus spp</i>	wombats
<i>Wallabia bicolor</i>	swamp wallaby

Eutherians

<i>Aepycerus melampus</i>	impala antelope
<i>Ailuropoda melanoleuca</i>	giant panda
<i>Alces alces</i>	moose
<i>Alouatta palliata</i>	howler monkey
<i>Antidorcas marsupialis</i>	springbok
<i>Antilope cervicapra</i>	blackbuck
<i>Bison bonasus</i>	European bison
<i>Bradypus tridactylus</i>	three-toed sloth
<i>Bradypus variegatus</i>	three-toed sloth
<i>Camelus dromedarius</i>	dromedary
<i>Canis familiaris dingo</i>	dingo
<i>Cervus elaphus</i>	red deer
<i>Choleopus didactylus</i>	two-toed sloth
<i>Connochaetes taurinus</i>	wildebeest
<i>Dasyprocta spp</i>	kongoni
<i>Dendrohyrax spp</i>	tree hyrax
<i>Dipodomys deserti</i>	desert kangaroo-rat
<i>Equus asinus africanus</i>	African donkey
<i>Gazella granti</i>	Grant's gazelle
<i>Gazella spekei</i>	Speke's gazelle
<i>Gazella thompsoni</i>	Thompson's gazelle
<i>Giraffa camelopardalis</i>	giraffe
<i>Halichoerus grypus</i>	grey seal
<i>Hippopotamus amphibius</i>	hippopotamus
<i>Hydrochoerus hydrochaeris</i>	capybara
<i>Hydropotes inercnis</i>	Chinese water deer
<i>Kobus ellipsiprymnus</i>	waterbuck
<i>Lama guanicoe pacos</i>	alpaca
<i>Lepus timidus</i>	snowshoe hare
<i>Litocranius walleri</i>	gerenuk
<i>Loxodonta africana</i>	African elephant
<i>Madoqua kirki</i>	Kirk's dikdik
<i>Microtus pennsylvanicus</i>	meadow vole
<i>Muntiacus reevesi</i>	Reeve's muntjac
<i>Nesotragus moschatus</i>	sun
<i>Oryctolagus cuniculus</i>	rabbit
<i>Ourebia oribi</i>	oribi
<i>Procavia habessinica</i>	rock hyrax
<i>Rangifer tarandus</i>	reindeer, caribou
<i>Rattus rattus</i>	black rat
<i>Sciurus carolinensis</i>	grey squirrel
<i>Sylvicapra grimmia</i>	grey duiker
<i>Taurotragus oryx</i>	eland antelope

Aves

<i>Ninox strenua</i>	powerful owl
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