The nutritional ecology of rodent pollinators of *Protea* in South Africa

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Introduction

Many African mammals feed on flowers. Many rodents eat flowers or flower-parts and even large mammals such as springbok, *Antidorcas marsupialis*, and giraffe, *Giraffa camelopardalis*, rely heavily on flowers as food at certain times of the year (SAUER, 1983; NAGY and KNIGHT 1994). In most cases, flower-feeding by African mammals is destructive and is of little or no benefit to the plant. However, in the fynbos biome in southwestern South Africa, rodents are important pollinators of a number of *Protea* species (family Proteaceae) which bear cryptic inflorescences close to the ground (ROURKE & WIENS, 1977; WIENS *et al.*, 1983) and there is increasing evidence that rodents are also important pollinators in the succulent Karoo biome (S.D. JOHNSON, pers. comm.). Although pollination by non-flying mammals is not a uniquely African phenomenon, the degree to which it occurs in the fynbos is exceptional and matched only in Australia, where the plants involved are usually from the Proteaceae or Myrtaceae (ROURKE & WIENS, 1977; REBELO and BREYTENBACH, 1987; CARTHEW and GOLDINGAY, 1997). Non-flying mammal pollination in the fynbos (unlike Australia) is carried out by generalist rodent species, such as *Rhabdomys pumilio* and *Aethomys namaquensis*, which also occur in many parts of the southern African subcontinent where such flowers are absent (WIENS *et al.*, 1983). However, the plants themselves often appear specialised for mammal pollination (REBELO and BREYTENBACH, 1987).

Flower-feeding mammals, regardless of their status as pollinators or predators, visit the flowers to obtain nutrition from flower parts and products. For small mammalian pollinators, the flowers may provide a substantial proportion of their diet (VAN TETS and WHELAN, 1997). However, there has been very little study to date on the nutritional benefits or the physiological difficulties associated with flower-feeding.

The African rodents involved in the pollination of *Protea* species are seasonal nectarivores, feeding on foliage and seeds for most of the year. The main food rewards, nectar and pollen, are available to them in winter, when energy requirements of small rodents are high. More predaceous flower-feeders which eat entire flowers will also extract energy and various nutrients from petals, bracts and other flower parts, and rodent pollinators sometimes consume the bracts of *Protea* inflorescences (ROURKE and WIENS, 1977; I.G. VAN TETS, unpubl. data). Nectar is a dilute sugar solution, while pollen has protein-rich cytoplasm encased within a thick multi-layered cell wall. Both these food sources present a number of physiological challenges that the flower-feeder must be capable of overcoming. For nectar feeders the sugar concentration and composition will be important. Choice of flowers is likely to be influenced by sugar preferences that may well in turn be related to the animal's physiological capabilities. Pollen feeders must be able to extract the protein-rich cytoplasm from the surrounding cell wall, and their ability to utilise the pollen protein will be strongly affected by its amino acid composition.

Nectar

The nectar of *Protea* is unusual in that it contains the pentose sugar xylose (VAN WYK and NICOLSON, 1995). The concentration of xylose ranges from 0-36% of total sugar in the 46 species of *Protea* for which data are available, and tends to be higher in mammal-pollinated species than in bird-pollinated species (NICOLSON and VAN WYK, 1998). Within the Proteaceae, this sugar is restricted to the closely related genera *Protea* and *Faurea*, and it is not known from any other floral nectars. Physiological studies related to xylose consumption by pollinating rodents are described below. Variation in nectar sugars at the plant level was examined in two mammal-pollinated species of *Protea:* in both *P. amplexicaulis* and *P. humiflora*, variation in sugar composition between inflorescences and between plants was less than that within an inflorescence (NICOLSON and VAN WYK, 1998).

The nectar of rodent-pollinated *Protea* species has a higher sugar concentration than that of bird-pollinated species (WIENS *et al.*, 1983; S.W. NICOLSON, unpubl. data). This may be correlated with the greater proportion of sucrose (as well as xylose) in the rodent-pollinated species. Regardless of whether the nectar concentration averages 20.7% or 36.1% (four bird-pollinated and three mammal-pollinated species respectively; WIENS *et al.*, 1983), the pollinator obtaining its energy requirements from large volumes of sugar solution faces osmoregulatory challenges, especially if the nectar is diluted by winter rainfall. Hummingbirds and sunbirds are subject to chronic diuresis (BEUCHAT *et al.*, 1990; LOTZ and NICOLSON, 1999). We have investigated the urine diluting ability of two rodent pollinators, the striped field mouse (*Rhabdomys pumilio*) and the Namaqua rock mouse (*Aethomys namaquensis*). When these mice were fed 0.1 M sucrose solution, equivalent to 3.5% (w/w), their urine osmolalities dropped to 30.5 ± 12.0 mOsm. kg^{-1} (mean ± SE) and 37.2 ± 9.5 mOsm. kg^{-1} respectively (I.G. VAN TETS, C.A. BEUCHAT & S.W. NICOLSON, in prep.). In contrast, the same individuals, when deprived of water and fed rat chow only, were able to concentrate their urine to 4915 ± 595 and 3416 ± 79 mOsm. kg^{-1} respectively. These nectarivorous rodents are thus both good concentrators and good dilutors, and indeed they may be subject to both water stress and water deprivation in their natural environment: although seasonal nectar feeders in the fynbos biome, they are also widespread in southern Africa, including desert regions. Our data do not support the suggestion by BADDOURI *et al.* (1987) that the diluting ability of desert rodents may be compromised by their good concentrating ability.

Sunbirds and sugarbirds show a strong aversion to the xylose in *Protea* nectar (JACKSON *et al.*, 1998a). We tested the sugar preferences of *Aethomys namaquensis*, using pairwise combinations of 30% (w/w) solutions of sucrose, glucose, fructose, xylose, and a mixture of equal parts of glucose and fructose (JOHNSON *et al.*, 1999). The tests were designed to control for side biases which are evident in nectarivorous birds (JACKSON *et al.*, 1998a) and also in the mice. The mice preferred sucrose to hexoses and hexoses to xylose but, unlike the birds, they were willing to drink pure xylose solutions. The order of sugar preferences corresponded to the relative proportions of the sugars in rodent-pollinated *Protea* species (NICOLSON and VAN WYK, 1998). The only previous study of the sugar preferences of non-flying mammalian pollinators is that of LANDWEHR *et al.*, (1990) on Australian possums, which do not encounter xylose-containing nectars.

The efficiency of xylose absorption and metabolism in *A. namaquensis* was assessed by measuring dietary intake, blood xylose levels, and output in urine and faeces (JOHNSON *et al.*, 1999). Table 1 shows data obtained over a two day period, during which the mice ingested a large amount of xylose (approx. 1 g per day). The apparent absorption efficiency can be calculated from dietary intake and urinary output as approximately 97%. This is comparable with the high absorption efficiencies of sucrose, glucose and fructose in a variety of nectarivorous birds (JACKSON *et al.*, 1998b). The high value in *A. namaquensis* contrasts with the xylose absorption efficiency of 53% measured previously in the Cape sugarbird (*Promerops cafer*) fed with a xylose / glucose mixture (JACKSON *et al.*, 1998b). The mice are therefore able to utilise the xylose in *Protea* nectar.

The xylose may be metabolised by intestinal bacteria (as occurs in ruminants), or it may be absorbed and then metabolised by the mice themselves. This latter possibility is supported by the observation of extremely low levels of xylose in both faeces and blood (Table 1). If hindgut fermentation is the primary method of xylose breakdown, a much higher level of faecal xylose would be expected, as faecal material that did not pass through the caecum should still contain xylose. Furthermore, if *A. namaquensis* itself is unable to metabolise absorbed xylose, then a much higher blood xylose level would be expected. Xylose is readily absorbed across the gut wall of rodents (SALEM *et al.*, 1965; ALVARADO, 1966). Its absence from the blood, coupled with the low level in the urine, suggests that it has been metabolised or converted into another chemical form after absorbtion. However, further work is necessary to truly distinguish between these two possibilities.

		DAY 1	DAY 2
Food	Xylose consumed (mg)	979 ± 82	855 ± 189
Urine	Xylose excreted (mg)	31 ± 7.2	25 ± 10.5
Faeces	Xylose excreted (mg)	0.43 ± 0.16	0.29 ± 0.08
Blood	Xylose concentration (mg / ml)	0.20 ± 0.04	No data

Mice were provided with 30 % (w/w) sucrose and rat chow.
All values are mean ± SE. n = 8 (except faeces on day 2: n = 4).

Table 1
Data used to calculate xylose absorption efficiency in *Aethomys namaquensis*.

It has previously been assumed that mammals other than ruminants absorb xylose but are unable to metabolise it: this is the basis of the xylose absorption test (ZILVA and PANNALL, 1984). Metabolism of nectar xylose has wider significance, because xylans (xylose polymers) are major components of the hemicellulose in plant cell walls and this pentose sugar could be an important metabolite for herbivorous rodents.

Pollen

WIENS *et al.* (1983) disregarded pollen as a reward for small mammals visiting *Protea* inflorescences, assuming that it was ingested during grooming. Pollen is often overlooked in studies of pollinator nutrition for a number of reasons. The pollinator may not ingest enough to gain a significant nutritional benefit, the pollen may be deficient in one or more essential amino acids (MARTÍNEZ DEL RIO, 1994), and the tough cell wall may render it indigestible (STANLEY and LINSKENS, 1974). However, it seems that these three objections do not apply to mammalian pollinators of Proteaceae in either Australia (LAW, 1992; VAN TETS and WHELAN, 1997; VAN TETS and HULBERT, 1999) or South Africa (VAN TETS, 1997; HUTCHINGS, 1997; VAN TETS *et al.*, 2000) and that the pollen of Proteaceae is a potentially useful source of nitrogen and protein for small mammals. It is also probable that rodents feeding destructively on flowers would also gain protein from this source.

Analysis of the faeces of four small mammalian species captured in mountain fynbos near Cape Town revealed that all were capable of digesting *Protea* pollen (VAN TETS, 1997). The samples were taken from Namaqua rock mice, *Aethomys namaquensis*, and Edward's elephant shrews, *Elephantulus edwardsii*, at a site where *Protea humiflora* was flowering, and from striped field mice, *Rhabdomys pumilio*, and pygmy mice, *Mus minutoides*, from a site with *P. subulifolia* flowers. Staining with cotton blue lactophenol resulted in a dark blue protoplast but left the cell wall unstained, and the percentage of grains from which the protoplast had been removed, even if only partially, was counted using a light microscope. Samples of pollen were also taken directly from the pollen presenters of *P. humiflora* and *P. subulifolia* and assessed in a similar manner. In the faeces, the mean percentage of empty or partially empty pollen grains ranged from 49-83% in the four mammal species, but less than 1% of the pollen grains taken directly from the flowers fell into this category.

Analysis of the amino acid composition of *P. humiflora* and *P. subulifolia* pollen using HPLC (HUTCHINGS, 1997) demonstrated that the amino acid deficiencies seen in the pollen of hummingbird-pollinated flowers in North America (MARTÍNEZ DEL RIO, 1994) were not apparent. For the North American flowers, methionine and lysine were typically absent or present only in very low quantities. *Protea* humiflora pollen contains 2.0% methionine and 5.5% lysine (percentage of total amino acids, in moles per mole) and *Protea subulifolia* 2.1% and 6.4% respectively. These values compare favourably with those of good protein sources (MOIR, 1994). It should be noted that only small quantities of amino acids are present in *Protea* nectar, whether from bird-pollinated or mammal-pollinated species (WIENS *et al.*, 1983).

To test the ability of these rodents to use pollen as a source of nitrogen, we conducted feeding trials on *Aethomys namaquensis* using commercially available *Eucalyptus* pollen, with a similar amino acid profile to the two *Protea* species, and casein (HUTCHINGS, 1997; VAN TETS *et al.*, 2000). The mice were fed diets in which varying amounts of the protein source – either pollen or casein – were suspended in an agar gel enriched with sucrose, fructose and glucose. At the end of each trial, the faeces were collected, dried and weighed, as was any uneaten food. Urine was collected under paraffin to prevent evaporation, and Kjeldahl analysis was used to determine the nitrogen levels in the food, urine and faeces.

From these data we were able to measure a number of digestive parameters. These included the apparent digestibility of the nitrogen (the proportion of the dietary nitrogen intake that was not lost as faeces), the biological value (the percentage of the absorbed nitrogen that is retained by the animal and not lost in the urine), and the maintenance nitrogen requirement (the nitrogen intake required to maintain nitrogen balance).

The apparent digestibility of the pollen nitrogen was, not surprisingly, significantly less than that of the purified protein (75.6 *vs.* 58.4% for pollen, $P < 0.05$, t-test). The amino acids in a purified protein are exposed to digestion much more readily than those bound in or protected by complex biological structures. However, on all other parameters the mice did significantly better on pollen than on casein. The biological value of pollen was 49% as opposed to 39% for casein ($P < 0.05$, t-test) and the dietary maintenance nitrogen requirements were 84 mg N. day^{-1} on pollen and 161 mg N. day^{-1} on casein. This is equivalent to 700 mg of pollen per day and is consistent with the expected nitrogen requirements for an animal of this size on a natural diet (VAN TETS *et al.*, 2000).

Conclusions

The nutritional ecology of the mammalian pollinators in the Western Cape has many similarities to that of the mammalian pollinators in similar ecosystems in Australia. It is difficult to compare the sugar preferences of pollinators in the two regions as xylose is not present in the nectar of Australian Proteaceae, but both *Aethomys namaquensis* in South Africa and *Tarsipes rostratus* in Western Australia exhibit preferences that reflect the sugar composition of the flowers on which they feed (LANDWEHR *et al.*, 1990; JOHNSON *et al.*, 1999). In both regions, pollen was once assumed to be eaten only as the result of accidental ingestion during nectar feeding or grooming (WIENS *et al.*, 1983) and to be of little or no nutritional significance (SMITH, 1982). However, it is now clear that not only is it eaten directly by many small mammals while feeding on flowers (RICHARDSON *et al.*, 1986; VAN TETS pers. obsv.), but that it is also, regardless of the motivation behind ingestion, a potentially valuable protein source for small mammals. This includes those, such as the rodent pollinators of *Protea*, which are not specialist flower feeders. Not only do mammalian pollinators digest a large proportion of the pollen they ingest but, in at least four instances, they can meet their nitrogen requirements on a relatively small quantity of pollen (LAW, 1992; VAN TETS, 1998; VAN TETS *et al.*, 2000). The importance of pollen as a dietary item for vertebrate pollinators is increasingly being recognised (GRANT, 1996; HERRERA & MARTÍNEZ DEL RIO, 1998).

These seasonal flower visitors have provided unexpected insights into general rodent physiology. We are now aware that rodents can digest xylose, a hitherto overlooked but presumably important source of energy for herbivorous rodents, and we have investigated the possible links between diluting and concentrating ability in small mammals. Flower products are clearly an important element of the diet of many rodents in the Western Cape and should not be overlooked in nutritional and dietary studies dealing with small mammals in other parts of Africa.

Acknowledgements

We thank all those who have helped with various parts of this research, in particular C. Beuchat, W. Brandt, K. Hutchings, S. Johnson, W. Stock and B.-E. van Wyk. I. G. van Tets was supported by a prestigious post-doctoral fellowship from the South African Foundation for Research and Development (FRD).

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on Gliridae, Anomaluridae and Pedetidae. This study confirms that the genus *Graphiurus* is clearly a member of the Gliridae family and reveals a strong affinity between Anomaluridae and Pedetidae. These two African families appear as a new lineage (suborder Anomaluromorpha) among sciurognath rodents as previously suggested by some morphological characters. This molecular result clearly contradicts morphological relationships deduced from the evolution of incisor enamel microstructure. Implications of molecular and morphological results are discussed in the light of paleontological data.

Keywords: Rodents — Classification — Molecular phylogeny — Palaeontology — Incisor enamel.

Behaviour, Physiology and Reproduction

I. G. Van Tets, S. W. Nicolson: "The nutritional ecology of rodent pollinators of *Protea*"

The nutritional ecology of rodent pollinators of *Protea* species in South Africa is reviewed. Sugar preferences of *Aethomys namaquensis* are correlated with the sugar composition of rodent-pollinated species of *Protea* and xylose, a pentose sugar found in *Protea* nectar, is more willingly consumed by the mice than by bird pollinators. The ability of *A. namaquensis* to metabolise xylose is an exciting new finding. At least two species of these seasonal nectarivores are capable of producing both remarkably dilute urine and highly concentrated urine in response to variation in water intake, and *A. namaquensis* is able to meet its nitrogen requirements on small quantities of pollen. *Protea* flowers are likely to be an important food resource for these animals in winter.

Keywords: *Protea* — Rodent — Nectar — Pollen — Pollination.

L. N. Bennett, N. Pillay: "Responses of male *Rhabdomys pumilio* to urine of females in different reproductive states"

The behavioural responses of male striped mice *Rhabdomys pumilio* to urine of cycling (dioestrus, oestrus), pregnant (mid- and late pregnancy), and postpartum oestrous females were studied in two-stimulus preference tests. It was predicted that males would prefer urine of receptive females to that of non-

Pedetidae. Cette étude confirme que le genre *Graphiurus* appartient bien aux Gliridae et qu'il y a une relation forte entre Anomaluridae et Pedetidae. Ces deux familles africaines constituent une nouvelle lignée (sous-ordre Anomaluromorpha) parmi les rongeurs sciurognathes, ce qui avait déjà été suggéré par des caractères morphologiques. Ce résultat moléculaire contredit les relations morphologiques déduites de l'évolution de la microstructure de l'émail des incisives. Les implications des résultats morphologiques et moléculaires sont discutées à la lueur des données paléontologiques.

Mots clés : Rongeurs — Classification — Phylogénie moléculaire — Paléontologie — Émail — Incisives

Comportement, physiologie et reproduction

I. G. Van Tets, S. W. Nicolson : « L'écologie nutritionnelle des rongeurs pollinisateurs de *Protea* en Afrique du Sud »

L'écologie nutritionnelle des rongeurs pollinisateurs de *Protea* en Afrique du Sud est passée en revue. Les préférences en sucres d'*Aethomys namaquensis* sont corrélées avec la composition en sucres des espèces de *Protea* pollinisées par les rongeurs, et le xylose, un pentose trouvé dans le nectar des *Protea*, est plus volontiers consommé par les rongeurs que par les oiseaux pollinisateurs. La capacité d'*A. namaquensis* à métaboliser le xylose est une découverte intéressante. Au moins deux espèces de nectarivores saisonniers sont capables de produire une urine soit très diluée, soit très concentrée, en réponse à la quantité d'eau consommée, et *A. namaquensis* peut subvenir à ses besoins en azote à partir de petites quantités de pollen. Les fleurs de *Protea* sont ainsi susceptibles de représenter une ressource alimentaire importante pour ces animaux en hiver.

Mots clés : *Protea* — Rongeurs — Nectar — Pollen — Pollinisation.

L. N. Bennett, N. Pillay : « Réponses de mâles de *Rhabdomys pumilio* à l'urine de femelles à différents états reproducteurs »

Les réponses comportementales de mâles de *Rhabdomys pumilio* à l'urine de femelles à différents stades de leur cycle reproducteur (di-œstrus, œstrus, milieu et fin de gestation, œstrus