

Banksia pollen in the diet of Australian mammals

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Mammals are frequent visitors to flowers in some Australian plant communities. Nectar is usually considered to be the food sought, because pollen is thought to be of low digestibility. This study compared the abilities of four non-flying mammal species to extract the protoplasts from *Banksia* pollen grains and quantified the amount of pollen in the diets of the species over 16 months. All four species were capable of extracting the protoplast from a large proportion of the pollen grains that they ingested: the mean percentage of empty *Banksia* pollen grains in the faeces ranged from 37% to 66%. *Banksia* pollen was a major component in the faecal samples from two species, *Cercartetus nanus* and *Petaurus breviceps*, between March and October. It occasionally comprised a large proportion of *Antechinus stuartii* faeces but was rare in the faeces of *Rattus fuscipes*. Other major components of faeces included invertebrates and plant material other than pollen and fungal spores. As the four mammal species tested were all from separate families and all capable of extracting the protoplast from a large proportion of the pollen grains, it is concluded that the extraction of pollen protoplasts by mammals may be widespread and may require no special adaptations.

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Pollination by mammals is reported to be common in some Australian systems (Turner 1982, Cunningham 1991, Goldingay et al 1991, Carthew 1993). Turner (1982) identified 25 marsupial species that visited flowers, many of which were likely to be important pollinators. Several megachiropteran bats are also major pollinators of a range of Australian plant species (Law 1992a).

Outside Australia, pollination by non-flying mammals has not been widely reported, although some primates are important pollinators (Ferrari and Strier 1992, Overdorff 1992, Gautier-Hion and Maisels 1994, Kress et al. 1994) and a number of South African rodents and insectivores are involved in *Protea* pollination (Wiens and Rourke 1978, Wiens et al 1983, Rebelo and Breytenbach 1987). A few rodent and marsupial species in South and Central America are also known to forage on flowers (Raven et al 1986). Bats are well known pollinators in many parts of the

world. Pteropodids (Megachiroptera) in Africa, Southern Asia and the South Pacific (Fleming 1993) and Phyllostomids (Microchiroptera) in the Americas (Howell 1974, Fleming 1993).

It is generally accepted that most of the mammals that visit flowers do so to feed on nectar (Turner 1982, Goldingay et al 1991, Fleming 1993). Nectar is rich in sugars and is unlikely to pose any digestive difficulties for most mammals. Pollen is rich in protein and other nutrients. It would seem to be advantageous for a mammal which takes nectar from a flower also to take pollen and thereby obtain these nutrients at little extra cost. However, a potential difficulty lies in the structure of pollen grains. A pollen grain has a thick outer wall (the exine) composed mainly of sporopollenin, a very resistant polymer, and a hard inner wall (the intine) composed of cellulose and pectin (Raven et al 1986). These walls must be penetrated before the protein-rich cell contents (the protoplast) can be reached and the

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walls are both highly resistant to digestion (Stanley and Linskens 1974, Raven et al 1986)

The strength of the pollen exine has led to the suggestion that the protoplast is difficult to extract (Hume 1982) and that special adaptations in mammalian digestive systems are required if protein is to be extracted from pollen grains (Stanley and Linskens 1974, Smith 1982, Turner 1984a,b, Martínez del Río 1994) Goldingay et al (1987) found that *Banksia* pollen grains in the faeces of two small mammal species (*Antechinus stuarti* and *Rattus fuscipes*) were mostly intact, supporting the view that pollen is indigestible. However, no data were provided to support this statement (Goldingay et al 1987). A third species (*Acrobates pygmaeus*) was reported in one study (Turner 1984a) as not digesting *Banksia* pollen grains, but subsequent studies have found large percentages of empty *Banksia* pollen grains in the hind gut and faeces of this species (Turner 1984b, Huang et al 1987).

Although only one marsupial species (the honey possum *Tarsipes rostratus*) is dependent on flowers for food (Turner 1983, Richardson et al 1986), there is good evidence that other flower-feeders ingest pollen. Large numbers of pollen grains have been found in the faeces of several mammal species including *Cercartetus nanus*, *Acrobates pygmaeus* (Turner 1984a,b, Huang et al 1987), *Cercartetus lepidus* (Ward 1992), *Petaurus breviceps* (Smith 1982), *Petaurus australis* (Goldingay 1990), *Antechinus stuarti* (Goldingay et al 1987), *Pteropus poliocephalus* (Parry-Jones and Augee 1991) and *Syconycteris australis* (Law 1992a). For *C nanus*, 65% of the *Banksia serrata* and *B spinulosa* pollen grains and almost 80% of the *B integrifolia* pollen grains that were found in the faeces were empty (Turner 1984b). Similarly, between 53% and 56% of the *Banksia* grains in the faeces of *S australis* were empty (Law 1992a, Woodside and Pyke 1995). Furthermore, laboratory studies have demonstrated that at least three mammal species (*P breviceps*, *S australis* and the American microchiropteran bat, *Leptonycteris sanbornii*) were able to maintain nitrogen balance on diets in which pollen was the only protein source (Howell 1974, Smith and Green 1987, Law 1992b).

Turner (1984b) and Arnould (1986) proposed a number of digestive adaptations that *C nanus* may use to extract protein from pollen grains. These included germination in the digestive tract, microbial digestion and chemically induced bursting of the pollen grains. However, a complex adaptation may not be necessary to enable pollen digestion. Many birds and insects can digest pollen (Paton 1981, Schmidt and Buchmann 1985, Richardson and Wooller 1990, Nicolson 1994). Furthermore, the observation by Arnould (1986) that *Banksia* pollen grains swell and burst at low pH, thus exposing the protoplast to enzymatic digestion in the intestine, suggests that a wide range of mammals may also be capable of breaching the pollen walls.

In the Barren Grounds Nature Reserve near Wollongong in south-eastern Australia, mammals are important pollinators of a range of *Banksia* species (Whelan and Goldingay 1986, Goldingay et al 1991, Carthew 1993). Carthew (1993) identified *C nanus* (Burramyidae), *P breviceps* (Petauridae) and *Antechinus stuarti* (Dasyuridae) as frequent visitors to the inflorescences of *B spinulosa*. *Rattus fuscipes* (Muridae) was identified as an occasional visitor (Carthew 1991).

These four mammal species are reported to have quite different diets. Seeds and insects are major components of the diet of *C nanus* (Arnould 1986). *Petaurus breviceps* is an arboreal species that feeds on plant exudates and invertebrates (Smith 1982, Howard 1989). *Rattus fuscipes* is usually regarded as a granivore/herbivore but hypogean fungi and invertebrates can comprise a large portion of its diet (Wheeler 1970, Watts 1977, Cheal 1987, Carron et al 1990). *Antechinus stuarti* is insectivorous (Hall 1980, Fox and Archer 1984). The aim of this study was to compare the ability of four mammalian flower visitors, spanning four families, to use pollen in their diets. This was approached by measuring the amount of pollen in the diets and by estimating the relative abilities of the species to extract protoplasts from pollen grains.

Methods

We trapped the four species of mammals in the Barren Grounds Nature Reserve (34°40'30"S, 150°43'15"E) over a 16-month period (March 1992–June 1993). Folding aluminium traps were placed in or near *Banksia* bushes. The traps were baited with creamed honey and a solution of honey dissolved in boiling water was sprayed on and around the traps. Microscopic examination confirmed that this honey used as a bait and attractant did not contain *Banksia* pollen.

To identify recaptured mammals, we recorded tail length, pes length, gender, weight and any physical peculiarities and marked the animals uniquely with a black permanent marker prior to release at the site of capture. Faecal samples collected from the traps were stored in glass scintillation vials in 70% ethanol. If an individual was captured more than once in a month, only one of the samples was used (chosen at random).

Approximately 10 mg of faeces, from the middle of each of two scats, was smeared onto a microscope slide. The first slide was stained with methyl blue (Phillips 1981) to highlight the pollen protoplasts. The second slide was stained with haematoxylin/ferric chloride (Schneider 1981) and counterstained with Giemsa's reagent (Cantwell 1981) to help identify the different faecal components.

Using a light microscope, 100 *Banksia* pollen grains along linear transects on each methyl blue slide were

recorded as either intact or empty. An intact pollen grain was defined as one that contained a protoplast within an exine which still had two caps (Fig 1a). An empty grain was defined as one that lacked one or both caps and from which at least some of the protoplast was removed (Fig 1b). If there were fewer than 100 *Banksia* pollen grains in the methyl blue slide, we also used the slide stained with haematoxylin/ferric chloride. Samples with <100 grains on the two slides were excluded from analysis. To determine the percentage of intact pollen grains prior to ingestion, we took pollen from the pollen presenters of one inflorescence from each of five plants from each of the four *Banksia* species found in Barren Grounds: *B serrata*, *B spinulosa*, *B ericifolia* and *B paludosa*. The pollen was spread on microscope slides and 100 pollen grains were recorded in the same manner as for the faecal smear.

The mean proportions of empty *Banksia* pollen grains in the faeces of the four mammal species were compared using a one-way ANOVA (Zar 1984). The data were arcsine transformed prior to analysis and



Fig 1 Intact and empty *Banksia* pollen grains. a - mainly intact *Banksia spinulosa* pollen grains taken from a pollen presenter. The two caps on either side of the grain are clearly visible and the grainy protoplast (P) can be seen, as can the outline of the exine (e). Two empty grains (E) are visible in the background. b - two empty *Banksia* pollen grains in the faeces of *A stuarti*. The caps are missing and only the exine is visible. The protoplast is absent.

Tukey's HSD tests (Zar 1984) were used to test differences between pairs of means.

The slide stained with haematoxylin/ferric chloride was used to determine the proportion of different dietary items in the faeces. Items in the faeces were allocated into one of six categories: 1) *Banksia* pollen, 2) pollen other than *Banksia*, 3) other plant material, 4) invertebrate, 5) fungi, and 6) unidentifiable. A cross-hair was placed in the eyepiece of the light microscope and items that fell under the ends of each cross-hair were counted. This process was continued along transects across the slide until a total of 100 items had been recorded.

Data were pooled into four groups of four months' duration. The first and last periods were March-June 1992 and March-June 1993. These periods corresponded with the early flowering season of *B paludosa*, *B spinulosa* and *B ericifolia*. The second period was from July 1992-October 1992. This matched the later part of the flowering season of *B paludosa*, *B spinulosa* and *B ericifolia*. The third period was from November 1992-February 1993. For the first half of this period, no *Banksia* plants were in flower and only *B serrata* plants were flowering in the second half. Because the data were highly skewed, a Kruskal-Wallis single factor analysis of variance by ranks (Zar 1984) was used to compare the relative abundance of *Banksia* pollen in the faeces of the four mammals in each period. A non-parametric multiple comparison test using Dunn's Standard Error (Dunn 1964, cited in Zar 1984) was used to determine pairwise differences.

Results

Only 0-2% of the grains sampled from the pollen presenters of fresh flowers were empty for any of the four *Banksia* species. In contrast, the mean percentage of empty grains was 66% ($\pm 3.3\%$) for *P breviceps*, 65% ($\pm 4\%$) for *C nanus* and 55% ($\pm 4.4\%$) for *R fuscipes* (Fig 2). *Antechinus stuarti* faeces contained a significantly lower percentage of empty grains than did faeces from the other three species (mean = 37% $\pm 2.7\%$, $p < 0.05$, Tukey's HSD). There were no significant differences in percentages of empty pollen grains among *P breviceps*, *C nanus* and *R fuscipes*.

Pollen occupied a large proportion of the volume of the faeces of *C nanus* in both the March-June periods and in the July-October 1992 period (Figs 3 and 4). Pollen was also abundant in the *P breviceps* samples for March-June 1992 and July-October 1992 (Figs 3 and 4). However, the March to June 1992 period only included three *P breviceps* samples. There were no *P breviceps* captured in March-June 1993. In every period, *C nanus* had a higher mean proportion of pollen in its faeces than the other three mammals, although it

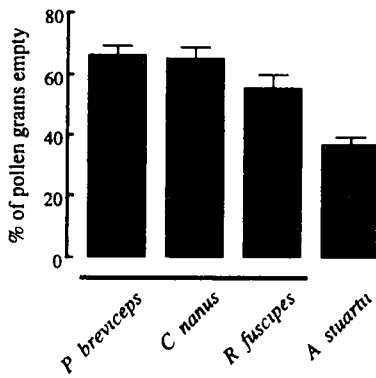


Fig 2 Percentage of *Banksia* pollen grains that were empty in the faeces of mammals captured in the Barren Grounds Nature Reserve, Australia. The percentage did not differ significantly between the three species that are underlined (error bars indicate standard errors, $n = 27$ for *P. breviceps* and *C nanus*, 21 for *R. fuscipes* and 37 for *A. stuarti*)

was never significantly higher than that of *P. breviceps* (Fig 3). In the November–February period, all four species excreted very little pollen and there were no significant differences between the proportions of pollen in the faeces of any of them (Fig 3c).

Antechinus stuarti faeces contained a small proportion of *Banksia* pollen in both March–June periods and in July–October 1992 (Figs 3 and 4). The proportion of *Banksia* pollen in the faeces of *A. stuarti* was signifi-

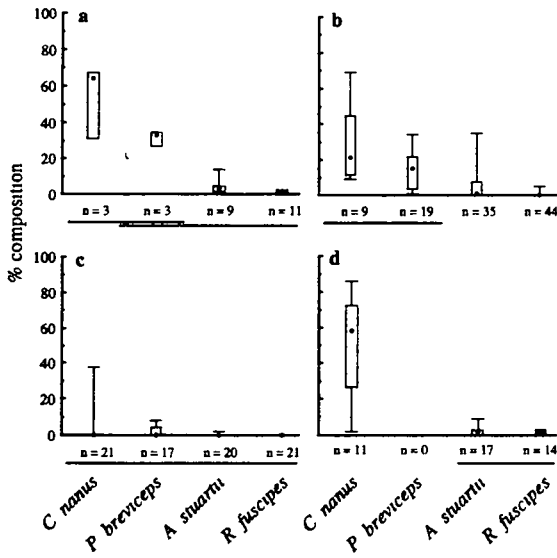


Fig 3 The percentage of faecal volume composed of *Banksia* pollen for four mammal species: a – March–June 1992, b – July–October 1992, c – Nov 1992–Feb 1993, d – March–June 1993. • indicates the median, the boxes indicate the range from the 1st quartile–the 3rd quartile and the bars indicate the full range. Species that share underlinings did not have significantly different proportions of pollen in their faeces ($p < 0.05$). *Petaurus breviceps* is not represented in d as none were captured during that period.

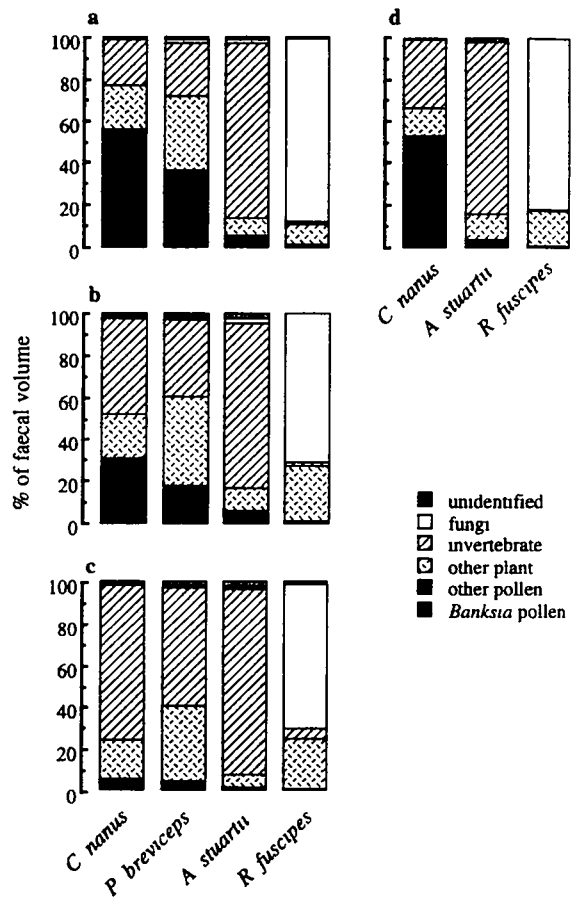


Fig 4 Mean percentage of faecal volume made up of different dietary components for four mammal species captured in the Barren Grounds Nature Reserve from March 1992–June 1993: a – March–June 1992, b – July–October 1992, c – Nov 1992–Feb 1993, d – March–June 1993. Sample sizes as in Fig 3.

cantly higher than in the faeces of *R. fuscipes* in the July–October period ($p < 0.05$, Fig 3b). *Rattus fuscipes* ingested the least *Banksia* pollen of the four species. The median percentage of the *R. fuscipes* faeces composed of *Banksia* pollen was invariably zero (Fig 3).

In addition to *Banksia* pollen, invertebrate fragments also represented a large proportion of faecal samples of *C nanus* (Fig 4). Moth fragments, particularly scales, were abundant and beetles and larvae were common. Plant matter other than pollen varied over the year. It consisted mainly of flower parts from March to October and mainly of seeds in the November–February period. The faeces of *P. breviceps* also contained large quantities of invertebrate fragments (Fig. 4) and moth scales were abundant. Plant fragments, particularly parts of flowers and leaves, were common, although seed fragments were relatively rare. Pollen grains from *Eucalyptus*, *Acacia* and several other genera were frequently found.

Table 1 Percentage of empty *Banksia* pollen grains in the faeces of mammals

Mammal	Pollen	mean %	SE	n	Reference
<i>T. rostratus</i>	<i>Banksia</i> spp	95–100	*	*	Richardson et al 1986
<i>C. nanus</i>	<i>B. spinulosa</i>	89.7	6.0	5	Huang et al 1987
<i>C. nanus</i>	<i>B. integrifolia</i>	78.6	6.1	18	Turner 1984b
<i>A. pygmaeus</i>	<i>B. spinulosa</i>	76.1	12.1	5	Huang et al 1987
<i>P. breviceps</i>	<i>Banksia</i> spp.	66	3.3	27	this study
<i>C. nanus</i>	<i>B. serrata</i>	65	7.6	6	Turner 1984b
<i>C. nanus</i>	<i>Banksia</i> spp.	65	4.0	27	this study
<i>C. nanus</i>	<i>B. spinulosa</i>	63.7	19.1	3	Turner 1984b
<i>S. australis</i>	<i>B. integrifolia</i>	55.8	4.7	22	Woodside and Pyke 1995
<i>R. fuscipes</i>	<i>Banksia</i> spp.	55	4.4	21	this study
<i>S. australis</i>	<i>B. integrifolia</i>	53	4	11	Law 1992a
<i>P. breviceps</i>	<i>B. spinulosa</i>	52.7	4.2	15	Goldingay et al 1987
<i>A. pygmaeus</i>	<i>Banksia</i> sp	39**	N/A	1	Turner 1984b
<i>A. stuartii</i>	<i>Banksia</i> spp.	37	2.7	37	this study
<i>A. stuartii</i>	<i>B. spinulosa</i>	<50	*	*	Goldingay et al 1987
<i>R. fuscipes</i>	<i>B. spinulosa</i>	<50	*	*	Goldingay et al 1987
<i>A. pygmaeus</i>	<i>B. spinulosa</i>	undigested	*	*	Turner 1984a

* not recorded ** = pollen from hind gut contents not faeces

Invertebrate fragments were the major component of *A. stuartii* faeces (Fig. 4). Moth scales were particularly common in faeces collected from March–October and the faecal samples containing large quantities of pollen invariably also contained large quantities of moth scales. Fragments from beetles were common in the November–February period. The faecal samples of *R. fuscipes* were primarily composed of fungal spores (Fig. 4). There was, however, a sizable proportion of plant matter present. This was mainly composed of fragments of bracken stems, although seeds, particularly those of *Gahnia sieberiana*, were common in the faeces from November–February.

Discussion

Banksia pollen was a major dietary constituent for only two of the species studied: *C. nanus* and *P. breviceps* and even for them it was not the sole protein source. Insects were common in the faeces of *C. nanus*, while *P. breviceps* would obtain protein from the wide variety of plant materials that it ate, as well as from invertebrates.

The proportion of plant material, including pollen, in *A. stuartii* faeces was higher than described in other studies (Hall 1980, Fox and Archer 1984, Dickman 1986) and it occasionally excreted relatively large amounts of pollen. However, it was clearly primarily insectivorous.

Banksia pollen composed <1% of the faecal samples of *R. fuscipes*. Fungal spores were consistently the major component of the faeces of this species (Fig. 4). Fungi are usually of only seasonal importance in the diet of *R. fuscipes* (Wheeler 1970, Cheal 1987, Carron et al 1990), although Cheal (1987) suggested that they select fungi when it is available. The constancy of the diet may be a local phenomenon, as Barren Grounds

supports a wide variety of fungi throughout the year, due to frequent rain and poor drainage (Wood 1987).

All four mammal species extracted the protoplast from some of the pollen grains that they ingested (Fig. 2), indicating that pollen was a potential source of protein for all of them. A substantial proportion of pollen grains in the faeces of *C. nanus* and *P. breviceps* had had the protoplast removed. Although pollen was not prominent in the diets of *A. stuartii* or *R. fuscipes* in this study, they did extract protoplasts from pollen grains. Contrary to the observation in Goldingay et al (1987), the percentage of empty grains in the faeces of *R. fuscipes* was not significantly different from that of *P. breviceps* and *C. nanus*. *Antechinus stuartii* extracted the protoplast from 37% of the grains it ingested.

Given the range of taxa represented by these four mammal species, and their dietary differences, it is probable that other mammals will also be able to digest *Banksia* pollen. Our results, and data from other published studies (Table 1), show that a variety of mammal species can remove the protoplast from a substantial proportion of the pollen grains. There was a large degree of variation between the results for some species, but there are several possible explanations for variability, including small sample sizes (e.g. Turner 1984b, Huang et al 1987) or variation in the viability of pollen at different sites. Inviably pollen is more readily digested than viable pollen (Arnould 1986, Wooller et al 1988).

Some mammals may have adaptations that enhance the digestibility of pollen. This is particularly likely in *T. rostratus*. When fed exclusively on nectar and pollen, it extracted 95–100% of the protoplasts from the pollen grains (Richardson et al 1986). There are suggestions in the literature of at least three possible adaptations: increased acid secretion in the stomach, a slow gut passage rate and hind gut fermentation.

Arnould (1986) suggested that stomach acid exposes the *Banksia* pollen protoplast to digestion in the small

intestine. If this is the case, then mammals which have a higher than normal concentration of acid-secreting cells in their stomachs will be able to extract the protoplast from a higher percentage of pollen grains (Law 1992a). The length of time that pollen spent in the intestine also increased the percentage of empty protoplasts for three species, *T. rostratus*, *C. nanus* and *S. australis* (Turner 1984b, Richardson et al 1986, Law 1992a). Therefore, mammals with a slower gut passage rate are likely to extract the protoplast from a higher proportion of pollen grains than those with a faster rate. Fermentation of pollen grains in a caecum may also raise the percentage of pollen grains that are digested. This is supported by measurements that found a higher proportion of empty *Banksia* grains in the caecum of an *Acrobates pygmaeus* individual than in its hind gut (Turner 1984b). Unfortunately, the only published study on the caecal flora of *A. pygmaeus* used mammals from an area where *Banksia* were rare (Salminen et al 1992). *Antechinus stuarti* is the only one of the four mammals studied that lacks a caecum (Hume 1982). This lack of a caecum may have been the reason for the significantly lower percentage of empty pollen grains in its faeces. As it has a very short and simple digestive tract (Hume 1982) it may also have a faster gut passage rate than the other mammals.

Although these sorts of adaptations may enhance pollen digestion, the study reported here shows that they are not essential. Even for the species which appeared to have little pollen in the diet, such as *A. stuarti* and *R. fuscipes*, significant numbers of pollen grains were digested. The ability to extract the *Banksia* pollen protoplast is therefore not limited to a small number of specialists and other studies of the diets of mammals that forage on flowers should not overlook pollen as a potentially important component of the diet.

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