CAN FLOWER-FEEDING MARSUPIALS MEET THEIR NITROGEN REQUIREMENTS ON POLLEN IN THE FIELD?

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Two arboreal marsupials, the eastern pygmy possum (*Cercartetus nanus*) and the sugar glider (*Petaurus breviceps*) have exceptionally low maintenance nitrogen requirements on pollen diets. This study compares their nitrogen requirements with the density of *Banksia* pollen that is available in the Barren Grounds Nature Reserve, New South Wales, a site where both species are known to forage on *Banksia* inflorescences. The pollen density was sufficiently high that both species were capable of meeting their maintenance nitrogen requirements on pollen whenever *Banksia* spp. were in flower. *C. nanus* required a smaller proportion of its home range than *P. breviceps* to do so and pollen was likely to be of much greater nutritional significance to both species in winter than in summer. This corresponds closely with the results of field studies comparing the diets of these mammals at different times of the year. Pollen is an important source of nitrogen for flower-feeding marsupials but its importance will vary between species depending on the marsupial's requirements, its body size and on the quantity of pollen that is available.

Key words: Eastern Pygmy Possum, *Cercartetus nanus*, Sugar Glider, *Petaurus breviceps*, *Banksia*, pollen, nitrogen, diet

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MANY mammalian species feed on flowers or flower products. For example, in Britain the dormouse (*Muscardinus avellanarius*) feeds on the anthers of hawthorn (*Crataegus monogyna*) in early spring (Richards, White, Hurrell and Price 1984) and in the Kalahari desert *Acacia* flowers are eaten in large quantities by larger mammals such as springbok, *Antidorcas marsupialis*, and giraffe, *Giraffa camelopardalis* (Sauer 1983; Nagy and Knight 1994). Although in many cases the plants receive no corresponding benefit, a range of mammal species including bats, rodents, marsupials, primates and insectivores are involved in the pollination of various plant species (Rebelo and Breytenbach 1987; Goldingay, Carthew and Whelan 1991; Ferrari and Strier 1992; Fleming and Sosa 1994; Carthew and Goldingay 1997).

The two flower products on which mammals are most likely to feed are nectar and pollen. Nectar, a sugar solution produced by many flowers to attract pollinators, may be a useful energy source for a small mammal and pollen may provide a source of protein. The pollen of some mammal-pollinated *Banksia* species contains over 30% crude protein (Turner 1984, Stace 1987). The bulk of the protein in a pollen grain is found in the cell contents, known as the protoplast, and this protoplast is encased within a hard cell wall that is extremely resistant to chemical breakdown (Raven, Evert and Eichhorn 1992). The strength of this cell wall has led to a belief that it is difficult for small mammals to extract nutrients from pollen (Hume 1982). Some dietary studies have identified pollen as a major component of faecal samples but discounted it as a possible source of nutrition because of this perceived difficulty (e.g. Smith 1982).

In recent years, it has become clear that many small mammals are capable of digesting pollen. Field studies report high densities of empty pollen grains in faecal samples (Turner 1984, van Tets 1997, van Tets and Whelan 1997). Laboratory studies show exceptionally low dietary maintenance nitrogen requirements for two marsupial species fed pollen: the eastern pygmy possum, *Cercartetus nanus* (3.2 mg N. day^{-1}, mass 25 g; van Tets and Hulbert in press), and the sugar glider, *Petaurus breviceps* (21.6 mg N. day^{-1}, mass 156 g; Smith and Green 1987). The aim of this study was to determine whether these low nitrogen requirements can be satisfied at different times of the year by pollen alone.

METHODS

Cercartetus nanus and *P. breviceps* both feed on *Banksia* inflorescences in the Barren Grounds Nature Reserve in south-eastern New South Wales (Goldingay et al.1991; Carthew 1993; Carthew 1994; van Tets and Whelan 1997). This reserve contains four species of *Banksia*: *B. serrata, B. ericifolia, B. spinulosa* and *B. paludosa*. For each of these species, the number of inflorescences produced per plant in each month was recorded. Twenty-four plants were chosen randomly from six sites within the reserve and the number of inflorescences containing open flowers on each plant was recorded every two weeks during 1994. Open inflorescences were marked to avoid double counting. Inflorescences that were recorded as open in two consecutive months were recorded as half an inflorescence in each month.

The quantity of pollen produced was calculated by measuring the mean mass of 50 intact pollen bundles, 10 from each of 5 randomly chosen *B. ericifolia* and *B. paludosa* plants, was also measured. The values recorded by Turner (1984) were used for the other two *Banksia* species. The mass of *Banksia* pollen produced per plant in each month in Barren Grounds in 1994 was determined as follows. The mean mass of pollen per flower was multiplied by the number of flowers per inflorescence which was obtained from Copland (1987). This was then multiplied by the number of inflorescences produced in the month in question and divided by the number of plants in the sample.

The density of each *Banksia* species was then estimated by randomly selecting a 10 m by 10 m quadrat in each of the six sites. The number of plants from each *Banksia* species that were found within the quadrats was recorded. A value of 0 was recorded for *Banksia* species that were present at a site but not within that site's quadrat. If a species was not present at the site, no value was recorded. The mean number of plants per quadrat was multiplied by 100 to obtain an estimate of the number of plants per hectare. This value was multiplied by the mass of pollen produced per plant in each month to calculate the mass of *Banksia* pollen produced per hectare.

The pollen requirements of *P. breviceps* and *C. nanus* were determined in the following manner. First, the mass of pollen required by the mammal was calculated. As the pollen mixture used in the study on *C. nanus* contained 120 mg of nitrogen per gram of pollen (van Tets and Hulbert in press) and was similar to the mixture fed to *P. breviceps* (both were predominantly *Eucalyptus*), this came to 26.7 mg of pollen per day for *C. nanus* and 180 mg per day for *P. breviceps*. Next, the mass of pollen required by the mammal per day was divided by the mass of pollen produced by an inflorescence to determine the minimum number of inflorescences required by an individual. This was multiplied by 30 to estimate the number of inflorescences required over a 30-day period. Then the minimum number of *Banksia* plants that the individual required was determined by dividing the number of inflorescences required by the animal by the number of inflorescences produced per plant in each month. Finally, the minimum area required by an individual to meet its needs on pollen was estimated by dividing the mass of pollen required per month by the mass of pollen produced per hectare.

RESULTS

The flowering periods observed and the number of inflorescences open per plant (Fig. 1a) corresponded with those previously observed in the neighbouring Budderoo National Park (Copland and Whelan 1989). *Banksia serrata* flowered in summer and the other three species flowered in winter. *Banksia serrata* produced considerably more pollen per inflorescence (Table 1) and more inflorescences per plant (Table 2) than the other three species. However, the other species were present in much higher densities. The mean number of *B. serrata* plants per hectare was only 150 (Standard Error = 150), while for *B. paludosa, B. spinulosa* and *B. ericifolia* it was 1370 (SE = 410), 1650 (SE = 690) and 2900 (SE = 1400) respectively. Consequently, the quantity of pollen produced per plant was highest in February (Fig. 1b) but the highest levels of pollen production per hectare (Fig. 1c) were in winter. The minimum number of plants from each species of *Banksia* whose total pollen production would be required by *C. nanus* and *P. breviceps* are shown in Table 2.

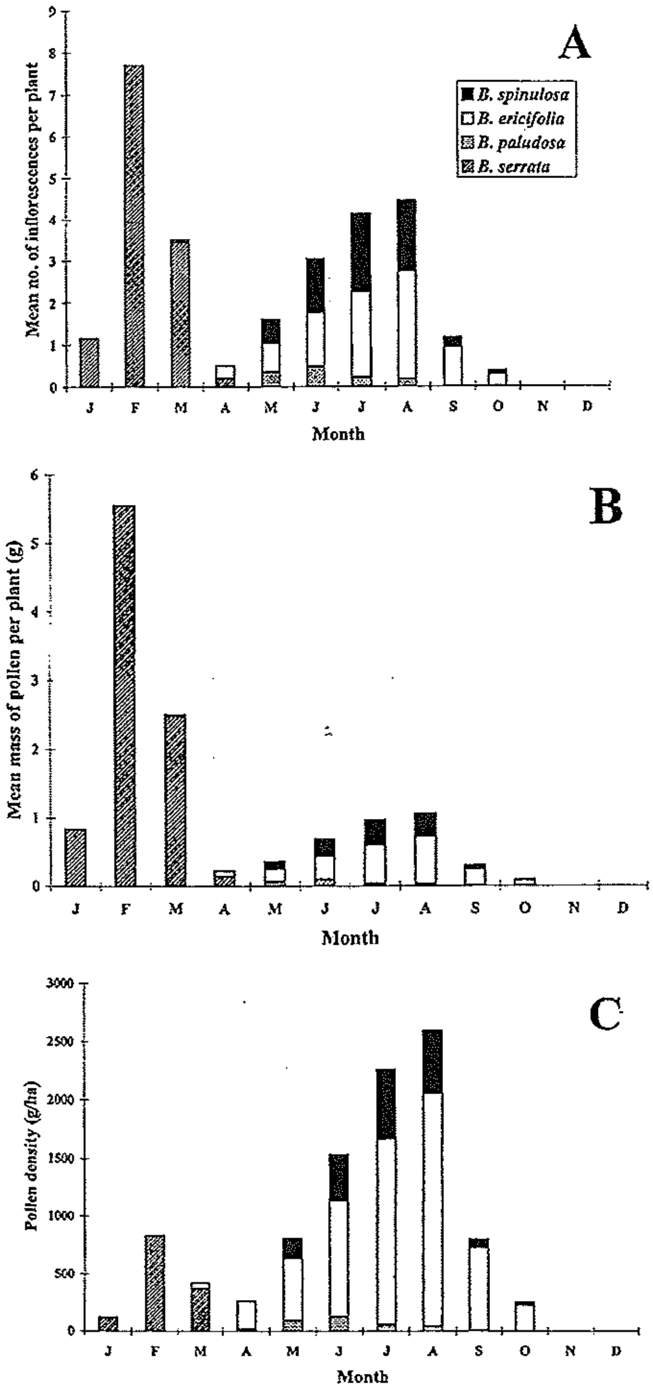

Fig. 1. Availability of *Banksia* pollen in the Barren Grounds Nature Reserve in 1994. A shows the number of inflorescences per *Banksia* plant, B the mean mass of pollen produced per *Banksia* plant and C, the mean density of *Banksia* pollen.

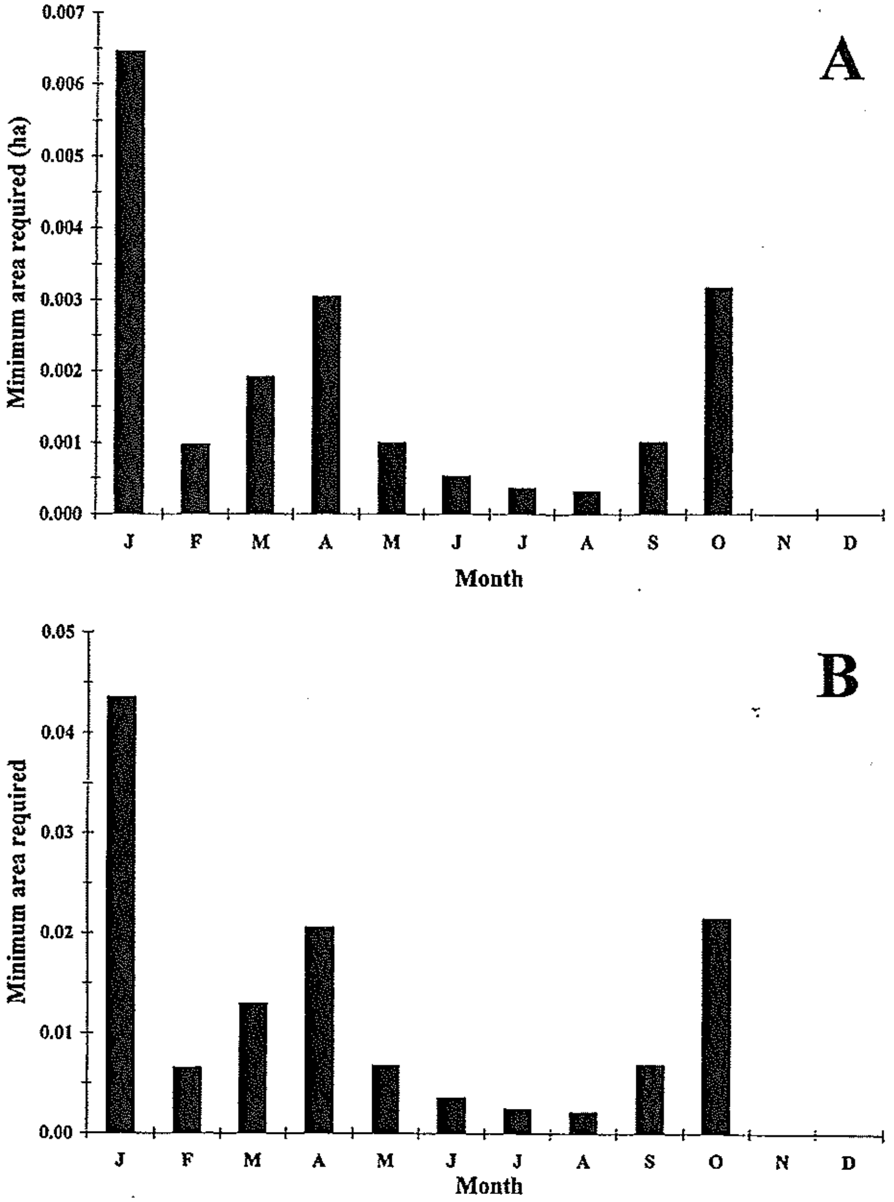

Fig. 2. The areas from which *C. nanus* (A) or *P. breviceps* (B) would have to collect the entire *Banksia* pollen production to meet its maintenance nitrogen requirements in the Barren Grounds Nature Reserve, based on the pollen density observed in 1994.

Figure 2 shows the minimum area required by these two marsupial species to meet their nitrogen requirements on *Banksia* pollen if all pollen was available to them. Predictably, the minimum number of *B. serrata* plants required is lower than the minimum for any of the other three species but the period in which the lowest minimum area is required is from June to August.

Species	Flowers / inflorescence*	mg pollen / flower	mg pollen / inflorescence
B. serrata	1722 ± 62 (5)	0.42 ± 0.021**	720
B. ericifolia	935 ± 42 (15)	0.29 ± 0.018	270
B. spinulosa	972 ± 28 (50)	0.2 ± 0.011**	190
B. paludosa	826 ± 19 (50)	0.23 ± 0.018	190

Table 1. Flower and pollen availability for inflorescences of four *Banksia* species. mean values are shown ± standard errors, ( ) indicates the number of inflorescences, * indicates values from Copland 1987, ** from Turner 1984.

	Pollen / inflorescence	Inflorescences required		Inflorescences / plant	Plants required	
	(mg)	*C. nanus*	*P. breviceps*		*C. nanus*	*P. breviceps*
B. serrata	720	1.1	7.5	7.7	0.1	1.0
B. ericifolia	270	3.0	20	2.6	1.1	7.7
B. spinulosa	190	4.2	28	1.9	2.2	15
B. paludosa	190	4.2	28	0.5	8.4	57

Table 2. The minimum number of *Banksia* plants whose total pollen production would be required by *C. nanus* and *P. breviceps* to maintain nitrogen balance on pollen over a 30 day period.

DISCUSSION

Although the number of plants and the areas required by *C. nanus* or *P. breviceps* appear low, it must be remembered that an individual animal would be very unlikely to be able to gather all of the pollen produced by an inflorescence. Conspecifics and other mammals would remove a sizeable proportion, while insects and birds would also take some pollen (Carthew 1993). Given this, how likely is it that *C. nanus* and *P. breviceps* can meet their nitrogen requirements on *Banksia* pollen?

Both animals appear capable of visiting sufficient plants, provided those plants are present in sufficient density. When *C. nanus* individuals were tracked using the spool and line method in Barren Grounds in winter, they visited an average of three *B. spinulosa* plants per night before the lines ran out (line length 165 m, Carthew 1994). In the same study, they also visited an equal number of *B. ericifolia* and about half as many *B. paludosa. Banksia spinulosa* was more common than *B. ericifolia* in the site of that particular study (Carthew 1994) so the visitation rate for *B. ericifolia* may be higher in other areas. The figures in Table 2 suggest that harvesting the pollen crop of 7 or 8 *Banksia* plants a night should provide *C. nanus* with a substantial proportion of its nitrogen requirements.

Petaurus breviceps has to visit considerably more plants than *C. nanus* (Table 2) but its mobility is considerably increased by its ability to glide and it should be able to obtain pollen from a much larger number of plants than *C. nanus*. Whether it in fact does so, and whether, if it did, this would be sufficient to meet a large portion of its needs is unclear. In the tracking study cited earlier (Carthew 1994), *P. breviceps* only visited an average of three *B. spinulosa* plants, and less than one *B. ericifolia* and *B. paludosa* per line - less than *C. nanus*. It is unlikely that the 265 m spools used were sufficient for an entire night's foraging but the result suggests that *Banksia* pollen may not be as important to *P. breviceps* as to *C. nanus*.

The estimations of the area required by *C. nanus* and *P. breviceps* to meet their nitrogen requirements on pollen in the Barren Grounds Nature Reserve (Fig. 2) provide a clearer indication of the relative ability of these two species to use pollen as a nitrogen source. *Cercartetus nanus* has a home range of approximately 0.7 ha (Ward 1990; Laidlaw and Wilson 1996). In July and August, *C. nanus* would require the *Banksia* pollen production of only 0.0004 ha to meet its maintenance nitrogen requirement and for the period May to September it would require less than the *Banksia* pollen production of 0.001 ha (Fig. 2a). *Cercartetus nanus* is clearly capable of meeting a substantial proportion of its maintenance nitrogen requirement in winter on *Banksia* pollen. During summer *Banksia* pollen, when available, is present in much lower densities (Fig. 2a). However, the minimum area required in January (0.0064 ha) is still less than 1 % of the home range of C. *nanus*. If harvested efficiently *Banksia* could still be an important supplementary source of protein for *C. nanus* during this period.

Petaurus breviceps is a much larger mammal than *C. nanus* and has considerably higher nitrogen requirements but, thanks to its size and its gliding ability it has a much larger home range (3.5 ha; Quinn, Smith, Green and Hines 1992). During winter, the minimum area required is again very low (0.0021 – 0.0035 ha between June and August) and, like *C. nanus*, *P. breviceps* should have little difficulty in meeting a large proportion of its nitrogen requirements on *Banksia* pollen during this period. In summer, a larger minimum area was required (0.044 ha or 1.3 % of its home range) but this was still sufficiently small that pollen feeding remains a possibility for *P. breviceps* at this time of the year.

As the maintenance nitrogen requirement measurements used mainly *Eucalyptus* pollen, these estimates are based on the assumption that the mass of *Banksia* pollen required is less than or equal to the mass of *Eucalyptus* pollen required. This is not an unreasonable assumption. The percentage of crude protein in the pollen of at least three of the four *Banksia* species (Turner 1984, Stace 1987) is higher than the percentage in the *Eucalyptus* pollens used in the laboratory experiments and, in the experiments on *C. nanus*, the percentage of empty *Banksia* pollen grains was higher than the percentage of empty *Eucalyptus* grains in their faeces (van Tets and Hulbert in press).

Free-living *C. nanus* and *P. breviceps* do not feed exclusively on flower products and the relative importance of different protein sources in the diet of these animals is likely to vary between regions and at different times of the year. For example, faecal samples taken from these two species in Barren Grounds between October and February usually contained a large quantity of insect fragments but little, if any, pollen. However, for the remainder of the year, both insect fragments and *Banksia* pollen grains were major faecal components and it was not unusual for the faecal pellets of *C. nanus* to be almost entirely composed of *Banksia* pollen grains (van Tets and Whelan 1997). When pollen is plentiful, its co-location with nectar would make it a desirable source of protein, particularly if other sources are in short supply. This may be one reason why many of the mammal-pollinated species of Proteaceae in both Australia and South Africa flower in autumn and winter. At other times and locations where insects are plentiful and suitable flowers scarce, insect protein may be of greater importance. Because of this, studies from one area that stress the importance of pollen in the diet of *C. nanus* in that area (Turner 1984; Huang, Ward and Lee 1987) are not really contradicted by the reports that it is less important or absent from the diet in others (Arnould 1986; Salminen, Pridmore, Adnaes and Ahokas 1992). These differences may simply reflect the different vegetation conditions at the site studied.

In winter, the energy requirements of a small mammal such as *C. nanus* are likely to be high. The ability of *C. nanus* to enter torpor or hibernation as a response to cold emphasises the importance of energy requirements to it in winter (Geiser 1993). The nectar provided by the various winter flowering *Banksia* species is a readily available source of easily digestible energy. While feeding on these inflorescences, *C. nanus* can also meet its nitrogen requirements concurrently, by eating pollen and by capturing the insects that visit the flowers. *Banksia* pollen is likely to be a major source of nitrogen for *C. nanus* at this time of the year. This is supported by the large proportion of *Banksia* pollen found in its faeces in winter (van Tets and Whelan 1997). In summer, warmer temperatures reduce the energy requirements of C. *nanus*. *Cer-*

cartetus nanus would also be able to gain more energy from sources other than nectar because of the increased activity of insects and possibly the increased availability of seeds. The lower density of *Banksia* inflorescences would reduce their attractiveness to *C. nanus* and the animals may use protein sources other than pollen during this period. This may explain the absence of *Banksia* pollen from all but a few of the *C. nanus* faecal samples between November and February (van Tets and Whelan 1997), even though *B. serrata* flowered in the second half of this period.

Given a sufficient density of pollen, both marsupial species appear capable of meeting their nitrogen requirements on pollen in the field. This is likely to be true of many small flower-feeding mammals, both marsupial and eutherian. However, what constitutes a sufficient density will vary between species, depending on their nitrogen requirements and their foraging behaviour. Their nitrogen requirements are in turn dependent on such factors as body size, chemical composition of the nitrogenous compounds in the pollen, and ability of the particular species to extract, absorb and retain those compounds. As it is clearly practical for small flower-feeding mammals like *C. nanus* and *P. breviceps* to meet a large proportion of their nitrogen needs on pollen, pollen should not be overlooked in dietary studies on similar animals.

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