Physiological Factors Affecting Pollen Use by Queensland Blossom Bats (Syconycteris australis)

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Physiological factors affecting pollen use by Queensland blossom bats (*Syconycteris australis*)

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Summary

1. The Queensland blossom bat (*Syconycteris australis*) is a specialist nectar and pollen feeder. Physiological factors that affect the efficiency of pollen use as a nitrogen source include pollen digestion and alimentary retention times. I examined how pollen of different forms affect these digestive constraints in blossom bats.
2. Twice as many pollen grains were empty in the intestine compared to the stomach, suggesting that the stomach is not the main site of pollen digestion. The percentage of pure *Banksia* pollen (~53%) digested was similar to that of pure *Callistemon* pollen (~55%). The percentage of *Banksia* pollen digested did not increase with time spent in the gut.
3. Pollen type affects the rate of food passage, in that the mean retention time (MRT) of *Callistemon* pollen (~50 min) is significantly shorter than that of *Banksia* pollen (~163 min). An experiment using a mixture of different-sized pollen grains, consisting of large *Grevillea* and *Banksia* and small myrtaceous pollen, showed that each pollen type had a similar passage time through the gut. This indicates that larger pollen is not selectively retained in the gut.
4. Gut passage rates for blossom bats are considerably faster than passage rates of other pollen feeders, but slower than fruit passage rates in larger flying foxes.

Key-words: Digestion, passage rate

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Introduction

Pollen is a source of nitrogen for many animals including lorikeets (Churchill & Christensen 1970), honeyeaters (Paton 1981; Wooller, Richardson & Pagendham 1988), honey possums (Turner 1984a; Richardson, Wooller & Collins 1986), New World bats (Howell 1974), Australian flying foxes (McWilliam 1986), pygmy possums (Turner 1984a, b), feathertail gliders (Turner 1984b; Huang, Ward & Lee 1987), *Antechinus* (Goldingay, Carthew &Whelan 1987) and sugar gliders (Goldingay *et al.* 1987; Smith & Green 1987), although the extent to which these animals rely on pollen varies greatly.

Physiological factors that can affect the efficiency of pollen use as a nitrogen source include pollen digestibility and gut passage rates. For example, facultative pollen feeders such as honeyeaters digest up to 44% of ingested pollen grains and have gut passage rates of 1–5 h (Wooller *et al.* 1988), whereas a nectar/pollen specialist like the honey possum (*Tarsipes rostratus*) can digest 95–100% of ingested pollen grains with peak gut passage rates of 6 h (Richardson, Wooller & Collins 1986). Each may represent a different strategy for utilizing pollen as a dietary source.

Flying foxes (Megachiroptera) are well-known blossom feeders (McWilliam 1986), although no studies have examined their physiological use of pollen. Flying foxes have fast gut passage rates of 12–34 min when fed fruit (Tedman & Hall 1985). Rapid food transit reduces the weight of gut contents during flight, but also results in the loss of a substantial proportion of nutrients. The effect of a rapid gut transit time on pollen utilization is not clear. As pollen is a highly complex structure (Stanley & Linskens 1974) further investigation is clearly needed to determine whether the processing of pollen differs from that of fruit in megachiropterans.

Pollen varies in structure and size from one plant species to another. As a consequence, the digestive constraints resulting from ingestion of one pollen species may be different from those of another. The Digestive Rate Model (Verlinden & Wiley 1989) suggests that the digestive constraints of different foods can affect foraging strategies. For example, greater pollen digestion or faster gut passage rates of one pollen species would increase efficiency of

nutrient processing and increase the time available for foraging. This has been demonstrated in frugivorous birds where gut transit times and digestibilities are constraints that are of importance in their foraging ecology (Worthington 1989).

The precise digestive mechanism that releases nutrients from the structurally resistant pollen grain is a further aspect of pollen utilization that is poorly understood. Digestion of germinating pollen grains in the stomach of nectarivores, by extrusion of pollen contents in an environment that is warm, sugary and slightly acidic, has been suggested for bats (Howell 1974), pygmy possums (Turner 1984a) and lorikeets (Churchill & Christensen 1970). However recent evidence for honey possums (Richardson *et al.* 1986), pygmy possums (Arnould 1986) and birds (Wooller *et al.* 1988) has shown that little or no digestion takes place in the stomach. Instead, digestion in the intestine was assumed to take place by enzymes that penetrate the germinal aperture of pollen grains and hence break down the pollen protoplast (Richardson *et al.* 1986; Wooller *et al.* 1988). The site of pollen digestion has not yet been investigated in bats.

In this study I investigated behavioural and physiological factors affecting pollen use by Queensland blossom bats (*Syconycteris australis*) Peters, 1867. These are small flying foxes (~18g) that are distributed throughout New Guinea and down the east coast of Australia as far south as the central coast of New South Wales. Very little is known of blossom bats, although they appear to specialize on a diet of nectar and pollen (Richards 1983), using their long brush-like tongue for feeding. Coastal heathlands, which produce copious amounts of nectar and pollen, provide suitable habitats for blossom bats.

I examined three aspects of pollen feeding behaviour in blossom bats. Firstly, I determined the extent of blossom feeding specialization by wild and captive bats to confirm that nectar and pollen are major dietary items of blossom bats. Secondly, I examined gut morphology and the site of pollen digestion. Lastly, I studied the effect of ingesting different pollen types and pollen in pure and mixed samples in relation to the percentage of pollen digested and mean retention times (MRT).

Materials and methods

CAPTURE AND HUSBANDRY

All experiments were carried out in the School of Biological Sciences at the University of Sydney in 1989 and 1990. I used six (two females and four male) blossom bats (17–21 g) that were netted in flowering *Banksia integrifolia* heathlands, in the vicinity of littoral rain forest, in the Iluka and Harrington areas of the north coast of New South Wales. The bats were acclimated to captivity in cages of 2m (length) × 1·5m (width) × 2m (height). Outside of experimental periods, bats were maintained on a liquid diet of mashed bananas, apple juice, sugar and 'Infasoy' protein (D. P. Woodside, personal communication). Approximately 20ml of this mix was provided per bat per day in 'guinea-pig' feeders positioned ~1·5m high in the cage. Fresh blossoms of a variety of species were also provided regularly, with fresh foliage for roosting. Temperature ranged from 20 to 24°C, humidity ranged from 70 to 80% and a light cycle of 12:12 D:N approximated natural lighting. All experiments began after the bats' body mass stabilized in captivity, about 4 months after capture.

Table 1. Food types offered to blossom bats in captivity

Food types	Observation†
Blossoms	
Banksia integrifolia (****)	+
Banksia ericifolia (****)	+
Banksia spinulosa (****)	+
Callistemon viminalis (***)	+
Callistemon salignus (***)	+
Melaleuca quinquenervia (**)	+
Acacia longifolia (*)	−
Acacia baileyana (*)	−
Pittosporum undulatum (*)	−
Erythrina indica (Coral tree) (****)‡	−
Fruits	
Ficus rubiginosa (Port Jackson fig)	−
Ficus macrophylla (Moreton Bay fig)	−
Musa sp. (banana — peeled)‡	−
Morus alba (mulberry)‡	−
Insects	
Tenebrio sp. (mealworms)	−
Lepidoptera (moths)	−

* Degree of nectar richness.
†+, Feeding observed; −, no feeding observed.
‡Plants introduced to Australia.

NATURAL AND CAPTIVE DIET

Faecal samples from wild caught bats were stained with malachite green and acid fuschin: this stains empty pollen grains green and full pollen grains red (Richardson *et al.* 1986). Comparison of faecal pollen with pollen reference slides and counts of the number of empty and full pollen grains (at least 50) identified the species of blossom fed upon and the percentage of grains found empty in the faeces.

The degree of dietary specialization was examined by presenting a variety of flowers, fruit and insects to bats in captivity (Table 1). One food type only was presented at the beginning of an observational night. All observations were carried out under low light levels before fresh food mix was added. Hence bats had not been fed for at least 12h and were hungry. Each food type was presented to bats on at least two independent occasions. Observations of food types ingested and feeding behaviour were recorded over a

7-month period. For instance, when flowers were presented details of nectar and/or pollen feeding were noted. Fruits were left for a number of days until they were over-ripe and began to fall from their branches.

GUT MORPHOLOGY AND THE SITE OF POLLEN DIGESTION

Eight wild caught blossom bats were dissected to examine the gross morphology of the alimentary canal. To ascertain which portion of the alimentary canal contributes most to pollen digestion, digesta samples were taken from the stomach, the length of the intestine and the rectum. These were stained as above. The percentage of empty pollen grains in each section of the alimentary canal was then counted.

PERCENTAGE DIGESTION AND MRT OF *BANKSIA* AND *CALLISTEMON* POLLEN

Banksia and *Callistemon* pollen represent the two predominant plant families that blossom bats feed on — Proteaceae and Myrtaceae (P.V. Driscoll & B.R. Irvin, personal communication). Pollen from these families differ in size and structure and thus may be processed differently in the digestive system. I chose *B. integrifolia* and *C. viminalis* to represent these families, because they are known food sources of blossom bats (B.S. Law, unpublished observation).

A 20-ml pulse dose of *Banksia* pollen and *Callistemon* pollen was administered orally to six randomly assigned bats; two male and one female receiving *Banksia* pollen and another two males and one female receiving *Callistemon* pollen. The pulse dose was given after 1 h of feeding on the standard liquid diet. This ensured that bats did not have empty stomachs, a factor that can reduce the retention times of pollen (Wooler *et al.* 1988).

I prepared the pulse dose by brushing pollen from pollen presenters (*Banksia*) or stamens (*Callistemon*) into separate beakers, each with 10 ml of water, until the solutions appeared cloudy. Arnould (1986) has shown in pygmy possums that inviable pollen is digested more than viable pollen and that inviable pollen is more abundant at the base of *B. integrifolia* inflorescences. As blossom bats probe the entire inflorescence for nectar when feeding (B.S. Law, unpublished observation), I also harvested pollen from the entire inflorescence. A dose of 2 ml of the appropriate pollen treatment was then orally administered to each bat with a syringe. A subsample of both pollen solutions was kept to ascertain the proportion of pollen grains that were naturally empty. A pure dose of pollen was examined because blossom bats often feed in areas with only a single plant species flowering.

During the experiment each bat was maintained in a small metabolic cage overnight. Faecal samples were collected on removable plastic sheets. The first faecal sample from each bat and any subsequent samples were collected overnight at half-hourly intervals. After the initial pollen dose was provided, each bat continued to feed through the night on the liquid food mix. All faeces collected were placed in pre-weighed vials and then reweighed to determine faecal mass and were subsequently stored at 4°C. Faecal samples were later mixed with malachite green and acid fuschin. The percentage of pollen digested is defined here as the proportion of empty grains resulting from digestion, calculated by subtracting the proportion of naturally empty pollen grains from the proportion of empty grains in the faeces (*Callistemon* = 9% naturally empty, $n = 155$ grains; *Banksia* = 18% naturally empty, $n = 450$ grains).

I have chosen MRT and minimum gut transit time (MGT) as measures of pollen passage rates through the digestive system. MGT is defined here as the time from ingestion of the pulse dose to the first appearance of pollen in the faeces (Warner 1981). MRT is defined as the time that the average pollen particle remains in the gut and can be calculated using the equation:

$$\text{MRT} = \sum_{i=1}^{n} m_i t_i / \sum_{i=1}^{n} m_i$$

where m_i is the amount of marker (pollen) excreted at the i^{th} defaecation, at time t_i after feeding of the marker (pollen), and n is the total number of defaecations (Warner 1981).

PERCENTAGE DIGESTION AND MRT OF MIXED POLLEN

Pure pollen samples are not consumed if feeding areas consist of a mosaic of plants flowering at the one time (P.V. Driscoll, personal communication). In this case a mixture rather than a pure sample of pollen will be ingested. Therefore, I examined the percentage digested and MRT of a commercial bee-collected pollen; this provided a mixture of three main pollen types — *Grevillea* (large and triangular ~80 μm long), *Banksia* (intermediate and sausage-shaped ~50 μm long) and Myrtaceae pollen (small and triangular ~25 μm long).

The experimental procedure used for the pure pollen experiment was followed for the analysis of mixed pollen. Only one experimental pollen treatment was used; therefore all six bats received a 2-ml pulse dose of the same pollen solution.

SAMPLING AND POLLEN COUNTING TECHNIQUES

Complete ingestion of the pulse dose could not be guaranteed, so it was not possible to measure directly

Table 2. Morphological characteristics of blossom bats and their alimentary tract

Measurement	Mean±SE (*n*)	
Stomach (mm)	21±4	(8)
Intestine (mm)	361±10	(8)
Forearm (mm)	41·0±0·3	(8)
Body weight (g)	19·7±0·8	(8)
Head–body length (mm)	49·9±10	(8)
Intestine/body length ratio	7·4	

the actual amount of pollen ingested in pulse dose experiments. Instead, the intakes of pollen were determined as the cumulative counts in faeces from the time of ingestion until the concentration of pollen fell to less than 0·1% of peak concentration (Cork & Kenagy 1989).

Acid fuschin and malachite green were thoroughly mixed with faeces to provide a 'faeces/stain slurry'. For a quantitative analysis of pollen excretion, the numbers of both digested and undigested grains were counted. This involved spreading one drop of faeces/stain mix from a vertical pasteur pipette (~0·01 ml) on a slide over a standard area the size of a coverslip. The mean number of pollen grains counted per area of coverslip was calculated by sampling five random fields of view for each slide and multiplying the mean of these fields of view by the number of fields of view in one coverslip. Further multiplication by the volume of faeces/stain mix added (0·01 ml) and division by the original faecal sample weight yielded a count of pollen per gram of faeces. Each sample was subsampled four times to give replicate counts. Where less than 10 pollen grains were counted for five fields of view, more fields of view were counted to give percentage digested data on at least 20 pollen grains.

Results

NATURAL AND CAPTIVE DIET

Direct evidence of pollen ingestion by blossom bats was obtained from microscopic examination of faecal samples ($n=11$) from wild blossom bats. Faecal samples were full with pollen grains and small amounts of hair. No other detectable substances were present in faeces. The predominant pollen present was *B. integrifolia*, the only significant nectar producer in the area from which bats were caught. The mean percentage (±SE) of empty pollen grains in the faecal samples was 72 ± 4%. This is not percentage digestibility, since the percentage of naturally occurring empty pollen grains on the *Banksia* inflorescences before ingestion, was not known.

Table 1 indicates that where choices were offered in captivity blossom bats fed on all blossoms that were rich in nectar. The introduced coral tree was an exception, as the nectar-rich flowers were not visited or investigated. No fruits or insects were eaten or investigated. Blossom bats probed blossoms for nectar, but not pollen. Pollen ingestion was observed only when bats thoroughly groomed their fur and wings after bouts of nectar feeding. Similar behaviour was also observed after feeding on the standard liquid diet from 'guinea-pig' feeders, even though pollen was absent from that diet.

GUT MORPHOLOGY AND THE SITE OF POLLEN DIGESTION

Morphometrics of the digestive tract are listed in Table 2. The oesophagus runs ventrally through the diaphragm to enter the cardiac portion of the stomach. The stomach, which forms a simple sac-like structure lying adjacent to the left lobes of the liver, leads via the pyloris into a broad duodenum. There was no morphological distinction between the small and large intestine; a caecum or appendix was absent.

Microscopic analysis of gut contents of six bats revealed no pollen germination tubes in any section. Pollen was either full, empty or partially empty, with progressively more empty grains found towards the end of the digestive system. The mean percentage of empty pollen grains counted was 25±5%, 47±6% and 59±9% in the stomach, intestine and rectum respectively, of the six dissected bats.

MRT AND PERCENTAGE DIGESTION OF PURE POLLEN DOSES

Results show that the type of pollen ingested significantly affected the rate of food passage in blossom bats. Rapid pollen transit times were recorded for both species of pollen, although pollen excretion was much faster for *Callistemon* pollen than for *Banksia* pollen (Figs. 1 and 2). The MGT ranged from 30 to 45 min (38±4 min, mean±SE, $n=3$) for *Callistemon* pollen and 39 to 145 min (95±31 min, mean±SE, $n=3$) for *Banksia* pollen. Ninety-four to 95% of *Callistemon* pollen was excreted in the first faecal sample, whereas only 60–70% of *Banksia* pollen grains were excreted in the first faecal sample. This pattern is reflected in a shorter MRT for *Callistemon* pollen, 50±1 min (range 48–51 min, $n=3$), than for *Banksia* pollen, 163±34 min (range 105–223 min, $n=3$) (Wilcoxin Rank Test — $Z=1·96$, $P<0·025$).

The percentage of *Banksia* pollen digested ranged from 39 to 69%, although the percentage of pollen digested did not change with the time spent in the gut (Fig. 2). As a result, all sampling times were pooled to give a mean of 53±4% for *Banksia* pollen. The percentage of *Callistemon* pollen digested could only be calculated for the first faecal sample, as 94–97% of all pollen grains were excreted at this time (Fig. 1). The percentage of *Callistemon* pollen digested

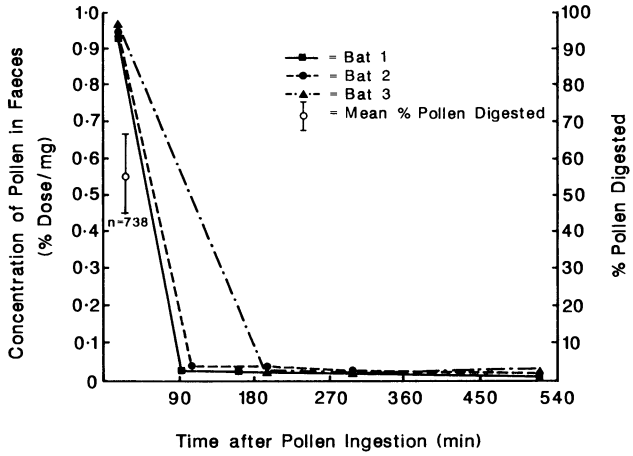

Fig. 1. Passage of pure *Callistemon* pollen through three individual blossom bats, represented as the change in concentration of pollen in faeces (% dose mg^{-1} faeces) against time. Mean % pollen digested is shown for the first faecal sample after the pulse done (n, total number of pollen grains counted, bars indicate ±SE).

ranged from 46 to 66%, with a mean of 55±11%, very similar to that of *Banksia* pollen.

MRT AND PERCENTAGE DIGESTION OF A MIXED POLLEN DOSE

The three pollen types in the pollen mix followed a similar pattern of passage to each other through the digestive system of blossom bats (Fig. 3). The overall pattern of mixed pollen excretion more closely resembled the excretion of pure *Banksia* pollen (Fig. 2) than pure *Callistemon* pollen (Fig. 1). The MGT of the mixed pollen dose ranged from 30 to 45 min (39±2 min, $n=6$). The mean percentage of total pollen excreted in the first faecal sample was 44±13% for *Grevillea*, 48±13% for *Banksia* and 39±15% for Myrtaceae pollen. The MRT of *Grevillea, Banksia* and Myrtaceae pollen were 142±41 min, 145±39 min and 143±39 min respectively, indicating that pollen of different sizes are not excreted independently when ingested in a mixed form. Statistical comparisons were not made because the passage of each pollen species was not independent when ingested as part of a mixture.

The percentage of pollen digested was calculated for the first faecal sample only, when the majority of pollen grains were excreted. Percentage pollen digested did not differ for Myrtaceae pollen (31±6%), *Banksia* pollen (37±7%) or *Grevillea* pollen (32±4%), although the percentage pollen digested was approximately 20% lower than percentage digestion calculated for pure pollen doses.

Discussion

Few animals specialize on a pollen/nectar diet. Specialization for blossom feeding in *S. australis* was

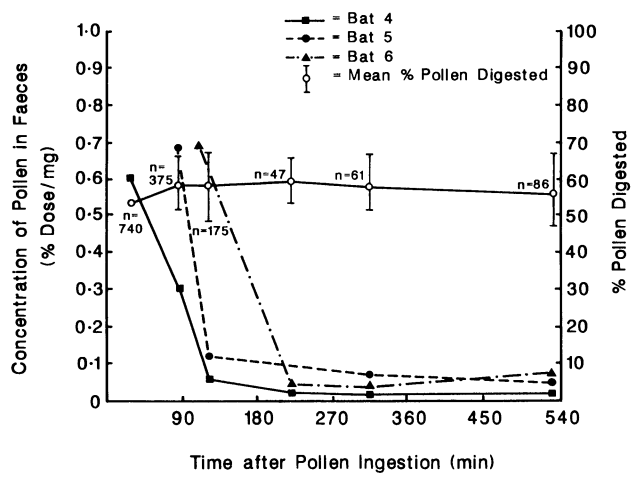

Fig. 2. Passage of pure *Banksia* pollen through three individual blossom bats, represented as the change in concentration of pollen in faeces (% dose mg^{-1} faeces) against time. Mean % pollen digested is shown for faecal samples at different time intervals (n, total number of pollen grains counted; SE are shown for sampling times with more than one faecal sample).

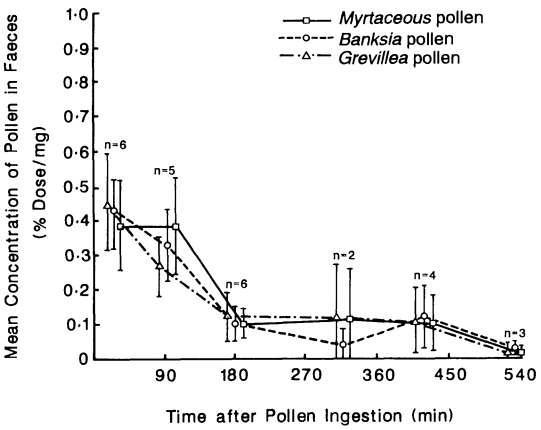

Fig. 3. Mean passage of mixed pollen through six blossom bats (n = number of faecal samples collected; bars indicate ±SE).

evident from faecal examination of wild caught bats; hair and pollen grains were the only detectable substances. Consistent with this were observations of blossom bats and their feeding preferences in captivity. Closer observations of their feeding behaviour show that blossom bats do not selectively feed on pollen, rather they probe deep into flowers to lap up nectar. Intensive grooming, after bouts of feeding, would remove sticky pollen that had adhered to the fur. Microscopic analysis of blossom bat fur shows that intricate scale-like structures are present (D.P. Woodside, personal communication), which may act as a pollen trap when blossom bats visit inflorescences to feed on nectar. Similar behaviour has been observed in pygmy possums, although Australia's other mammalian flower-feeding specialist, the honey possum, will directly eat pollen from flowers (Turner 1984a). Although blossom bats do not eat pollen directly from blossoms, the high percentage of empty grains in faecal samples of wild caught bats indicates that the digestive system of blossom bats is capable of utilizing pollen as a source of nitrogen (see concluding paragraph).

Blossom bats have a simple, relatively undifferentiated digestive system, which is typical of flying foxes (Tedman & Hall 1985), birds (Wooller *et al.* 1988) and the honey possum (Richardson *et al.* 1986). The high intestine/body length ratio in flying foxes (Tedman & Hall 1985), maximizes the exposure of digesta to intestinal cells where the majority of pollen digestion appears to take place. The lack of germinating pollen grains in the stomach suggests that it does not act as a germination chamber. Although the stomach contains more than half (25%) the percentage of empty pollen grains found in the intestine (47%), a large proportion of this may be accounted for by the unknown proportion of naturally occurring empty pollen grains on inflorescences. For example, 18% of *Banksia* pollen grains were empty in the freshly prepared pure pulse dose. Assuming little pollen digestion takes place in the stomach, then the mode of pollen digestion would most likely involve direct enzymatic digestion of the pollen grain through pores in the exine coat (Arnould 1986; Richardson *et al.* 1986). Arnould (1986) has shown that rupturing of pollen apertures increases with decreasing pH in *in vitro* tests. It is possible that the high concentration of acid secreting parietal cells found in the stomach of flying foxes (Tedman & Hall 1985) and macroglossine bats (Forman 1990) weaken the germinal apertures of pollen grains, thereby facilitating pollen digestion in the intestine.

The percentage of pollen digested by blossom bats is similar to other pollen eaters such as pygmy possums (20–70% — Turner 1984a; Arnould 1986), sugar gliders (53% — Goldingay *et al.* 1987) and honeyeaters (up to 44% — Wooller *et al.* 1988). However, these are all considerably less than the 95–100% of pollen digested by honey possums (Richardson *et al.* 1986). Honey possums have a relatively slow passage rate, with the percentage of empty grains in their faeces, linearly related to its length of time in the gut. In comparison, the percentage of *Banksia* pollen grains digested by blossom bats was not related to the length of time in the gut.

Pulse dose experiments, which account for the proportion of naturally empty pollen grains, have not previously been used to investigate the digestion of different pollen types. In blossom bats, *B. integrifolia* and *C. viminalis* pollen were not differentially digested. The mixed dose pollens of *Grevillea, Banksia* and Myrtaceae were also similar in the proportions digested, but were 20% less digestible than pure pollen samples. The mixed dose consisted of bee-collected pollen, which is treated with inhibition factors by bees (Stanley & Linskens 1974) and this may lower the amount digested by bats. These results indicate that there is little evidence for differential digestion of different pollen types.

Previously, however, Turner (1984b) found 74% of *Eucalyptus* pollen empty in the faeces of *Acrobates*, but that *B. spinulosa* pollen, also present, was not empty. In contrast, Huang *et al.* (1987) found that 89% of *B. spinulosa* pollen were empty in *Acrobates* faeces. Such apparent variability has been explained by differences in the proportion of inviable to viable pollen ingested (Arnould 1986; Wooller *et al.* 1988). Inviable pollen is more digestible and more common on the base of *B. integrifolia* inflorescences (Arnould 1986). However, nectar is usually widely distributed on these inflorescences (McFarland 1985), and blossom bats do not concentrate their feeding on a particular portion of the inflorescence (B.S. Law, unpublished observation). Differential pollen digestion may therefore result when variable proportions of viable and inviable pollen are ingested. An additional explanation for apparent differential pollen digestion, may be variability in the amount of naturally occurring empty grains on inflorescences. If

this varies from one plant to another, then the amount of empty grains found in the faeces will also vary, assuming that pollen digestion remains constant. Turner (1984a), for example, found 95% ($n=500$) of pollen grains were full on fresh *B. integrifolia* inflorescences; however in preparing the pulse dose for *B. integrifolia* I found only 82% ($n=450$) to be full.

Gut passage rates, as well as digestibility, can affect an animal's foraging ecology (Worthington 1989). In general, blossom bats have considerably faster passage rates than other pollen feeders, such as honey possums (Richardson *et al.* 1986), pygmy possums (Arnould 1986) and honeyeaters (Wooller *et al.* 1988). Fast passage rates are characteristic of the flying fox family, fruit having transit times of 12–34 min (Tedman & Hall 1985). In comparison, the minimum passage rate of pollen in blossom bats is slower, ranging from 30 to 95 min. Moreover, blossom bats are considerably smaller and therefore would have higher mass-specific metabolic rates and lower absolute gut capacities than the larger flying foxes. Pollen utilization, therefore, appears to require more time than fruit utilization in megachiropterans. Many interpretations of flying fox foraging ecology have been based on the constraints of their digestive physiology as determined on fruit diets (Thomas 1984; Stellar 1986). Such interpretations should also consider the importance of protein-rich pollen in their diet.

The type of pollen ingested by blossom bats significantly affects gut retention time. Larger pollen had longer MRT than smaller pollen; however there was considerable variability in the MRT of these pollen types. Such variability may be a consequence of variable rates of food ingestion following the pulse dose of pollen, given that food passage is known to be greatly influenced by the rate of food ingestion in fruit-eating manakins (Worthington 1989). Even with this variability, pure *Callistemon* pollen had a significant shorter MRT than pure *Banksia* pollen. This is perhaps due to the larger particle size of *Banksia* pollen, which is almost twice the size of *Callistemon* pollen. Large particle size and high fibre content are known to increase the retention time of food (Sibly 1981; Warner 1981).

Mechanisms for selective retention of large digesta particles are found in 'colon fermenters' (Hume 1989), and were investigated in blossom bats by following the passage of different-sized pollen in a mixed dose. Passage of large (*Grevillea* and *Banksia*) and small (myrtaceous) pollen grains did not differ in the mixed dose, indicating that neither size was selectively retained. Large pollen grains did, however, slow the passage of smaller pollen grains, indicating that pollen size is important in determining passage time. A consequence of this is that bats feeding on blossoms with large pollen grains will have significantly longer pollen passage rates compared to bats feeding on blossoms with smaller pollen grains. For example, blossom bats feeding on pure *Callistemon* pollen will be able to process and absorb nitrogen at a significantly faster rate than bats feeding on either pure *Banksia* pollen or a mixed diet containing some *Banksia* pollen, perhaps increasing time available for foraging (Verlinden & Wiley 1989).

Can blossom bats extract enough nitrogen from pollen when MRT is relatively short and only about 50% of ingested pollen grains are digested? The New World nectarivorous bat, *Leptonycteris sanborni*, can remain in positive nitrogen balance on a nectar and pollen diet (Howell 1974); however sugar gliders (*Petaurus breviceps*) are the only animals for which daily nitrogen requirements have been experimentally determined on a pollen diet. In comparison to blossom bats, sugar gliders have slow pollen passage rates (~24h; Smith & Green 1987). Clearly detailed examination of the daily nitrogen requirements of a pollen and nectar specialist, with rapid gut passage rates, is needed. The blossom bat can in fact remain in positive nitrogen balance and gain weight on a diet of only sucrose and pollen (Law 1992).

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