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FEEDING BEHAVIOUR OF BIRDS AND MAMMALS ON FLOWERS OF *BANKSIA GRANDIS* AND *EUCALYPTUS ANGULOSA*

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To resolve current controversies about birds versus mammals as pollinators of Australian plants, it is essential to observe animals feeding in the wild and examine pollen on stigmas after flowers have been visited. In practice, this has been problematical because all the mammals known to feed on flowers are thought to be nocturnal and difficult to observe. Here, we report the discovery at Cheyne Beach in Western Australia of a population of honey possums (*Tarsipes rostratus*) that feeds in daylight as well as at night. These honey possums feed much slower than white-cheeked honeyeaters (*Phylidonyris nigra*) on inflorescences of *Banksia grandis,* whereas they feed at roughly equivalent rates on flowers of *Eucalyptus angulosa.* The relationship of these feeding rates to pollination efficiency requires further investigation. Honeyeaters may be less sedentary than honey possums and therefore account for more outcrossing between plants. Honey possums preen pollen from their bodies more often than do honeyeaters. This may also influence the amount of outcrossing that occurs. Further study of the Cheyne Beach animals and their food plants is advocated.

INTRODUCTION

As increasing attention has focused on vertebrate pollinators in Australia, it has become apparent that many plants attract both birds and mammals to their flowers (Morcombe, 1968; Carpenter, 1978; Armstrong, 1979; Ford *et al.,* 1979; Wiens *et al.,* 1979; Hopper, 1980; Turner, this volume). The resolution of the relative importance of birds and mammals as pollinators of these plants provides a challenging field for investigation, particularly because the subject has already attracted a certain amount of controversy (e.g. Rourke & Wiens, 1977; Wiens *et al.,* 1979; Holm, 1978; Carpenter, 1978; as against Ford *et al.,* 1979; Armstrong, 1979; Hopper, 1980).

Pollination involves the transfer of pollen from anthers to stigmas.* Where two or more vectors are involved in the process, their relative importance as pollinators may be assessed by comparing the number of pollination events they effect per unit time (Primack & Silander, 1975). This parameter will be influenced by a complex of factors including the rate at which flowers are visited, the size, shape and orientation of feeding animals and the flowers involved, and the size and placement of pollen loads. Measurement of several of these factors requires observation of animals feeding in the wild, a difficult proposition in the case of Australia's nocturnal nectarivorous mammals. Here, we report a situation where the difficulty of strictly nocturnal feeding by mammals does not apply.

Cheyne Beach, on the south coast of Western Australia, first achieved recognition as a place where nectarivorous mammals and birds may be studied through the work of Morcombe (1967), 1968. He rediscovered a rare marsupial, the dibbler (*Antechinus apicalis*) there in 1966, and also commented on the profusion of wildflowers that provide a year-round nectar supply to both birds and mammals at the beach. Subsequently, Hopper (1980) reported a study undertaken by us in March 1979 on the bird and mammal pollen vectors in *Banksia* communities at Cheyne Beach. It was found that honey possums (*Tarsipes rostratus*) and three species of meliphagid birds all carried the pollen of the dominant flowering species of *Banksia, Adenanthos, Lambertia* (Proteaceae), *Beaufortia* and *Calothamnus* (Myrtaceae), and appeared to feed without preference on them.

*Subsequent events, such as pollen germination, pollen tube growth down the style, fertilisation etc., are conventionally excluded from the definition of pollination.

In this paper we present data from a follow-up study in November 1979, when we made the fortuitous discovery that normally nocturnal honey possums feed in daylight under the cool and cloudy conditions that prevail in the area at this time of year. This enabled a direct comparison of the feeding behaviour of these nectarivorous mammals with that of white-cheeked honeyeaters (*Phylidonyris nigra*) on two of the major summer-flowering plants at Cheyne Beach, *Banksia grandis* and *Eucalyptus angulosa*.

Description of plants and animals studied

Banksia grandis Willd. (Mangite or Bull Banksia) is a small tree up to 10 m tall, confined to the forests and coastal woodland areas of south-western Australia (Holliday & Watton, 1975; George, 1981). In south coastal areas such as at Cheyne Beach it is usually stunted (1-3 m tall) but occurs as a scattered emergent in dense low heath (Figure 1a). The species has large dentate leaves up to 50 cm long. It flowers in late spring to early summer, producing the largest inflorescences in the genus. These are yellow, cylindrical, up to 40 cm long and 10-12 cm in diameter. An average of 4700 flowers per inflorescence are produced at Cheyne Beach (Table 1). Styles are stiff, straight at their tips and 31–55 mm long. Flowers on tagged inflorescences opened at the rate of 144 per night and 246 during daylight, suggesting that it takes 12 days for an average inflorescence to complete anthesis (I. Abbott, pers. comm. established a similar period for the average life of inflorescences of *Banksia grandis* in the jarrah forest). Individual plants usually carried only one or two inflorescences in flower during the study period. No quantified data are available on nectar production of *B. grandis* but it was observedly copious during daylight and at night. Near Perth, the species is known to be an important nectar resource for red wattlebirds (*Anthochaera carunculata*), little wattlebirds (*A. chrysoptera*), New Holland honeyeaters (*Phylidonyris novaehollandiae*), western spinebills (*Acanthorhynchus superciliosus*) and yellow-throated miners (*Manorina flavigula*) (Rooke, 1979; Whelan & Burbidge, 1980; Hopper & A.H. Burbidge unpubl. data). Honey possums have been recorded feeding on *B. grandis* at Manypeaks (Wiens *et al.*, 1979) and Millbrook Nature Reserve (Hopper, 1981) in the Albany district. No published observations on potential insect pollinators of *B. grandis* are available, but I. Abbott (pers. comm.) has observed *Apis mellifera* and native hymenopterans on inflorescences in the jarrah forest. At Cheyne Beach, insect activity observed during the observation periods reported below was limited to an occasional moth observed harvesting nectar soon after sunset.

*Eucalyptus angulosa** Schau. is a multi-stemmed mallee, up to 5 m tall, of the south coastal regions of Western Australia and of South Australia (Chippendale, 1973). It occurs in small isolated groves at Cheyne Beach emergent from dense low heath (Figure 1b). From August to December, individual plants carry several hundred flowers borne on the outside of the canopy in inflorescences of up to seven flowers. Peduncles supporting the inflorescences are erect, flattened and 1.5-2.5 cm long. Each flower is subtended by a short (4 mm) pedicel. The deeply ribbed hypanthium is green and measures up to 1.5 cm long. The style is short (11-13 mm) and barely emergent from the orifice because the ovary roof is sunk deep (6-7 mm) within the hypanthium. The orifice is *c.* 10 mm in diameter at the rim. A flat-topped array of cream stamens splays up and outwards from the rim to a maximum diameter of 45 mm. Individual stamens range in length from 16 mm near the outside of the array to 4 mm for those located on the inner side of the rim. Anthers are carried up to 8 mm higher on the flower than the stigmatic tip of the style. Again no

*In some treatments this species is included in *Eucalyptus incrassata* Labill.

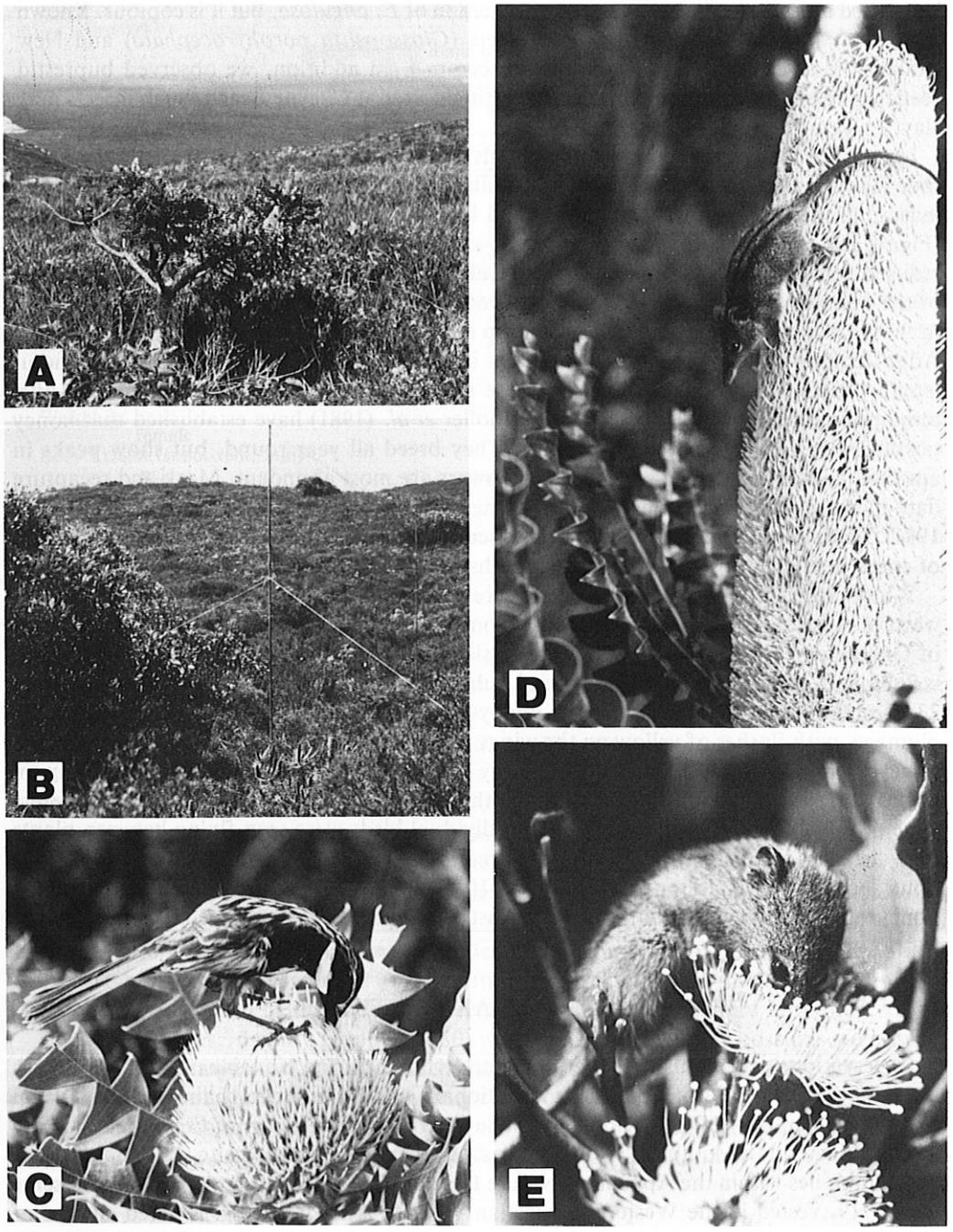

Figure 1. Photographs of plants and animals studied at Cheyne Beach. **a:** stunted *Banksia grandis* shrub 2 m tall, emergent from dense low coastal heath (photographed at Two Peoples Bay in February after flowering had finished); **b:** three isolated clumps of *Eucalyptus angulosa* 2–3 m tall, emergent from dense low heath; a mistnet used to capture honeyeaters for pollen sampling is to the right of the *E. angulosa* in the foreground; **c:** white-cheeked honeyeater (*Phylidonyris novaehollandiae*) feeding on nectar of *Banksia baxteri,* an important food plant in autumn at Cheyne Beach; **d:** honey possum (*Tarsipes rostratus*) on a large cylindrical inflorescence of *Banksia grandis*; **e:** honey possum feeding on nectar of *Eucalyptus angulosa.*

quantified data are available on nectar production of *E. angulosa,* but it is copious. Known pollinators include purple-crowned lorikeets (*Glossopsitta porphyrocephala*) and New Holland honeyeaters (B.J. Newbey, pers. comm.). In addition, we observed buprestid beetles, a few wasps and some moths harvesting nectar at Cheyne Beach. Such insects may play a role in pollination.

Honey possums are small agile marsupials confined to south-western Australia, where they favour heath, scrub and open low woodlands on sandy soils. They weigh 7-20 g when mature (Table 2; Wooller *et al.,* 1981) and have three distinctive stripes along the back (Figure 1d). Adaptations to a diet of nectar and pollen include an elongated snout, highly reduced dentition, brush tongue and a thin-walled diverticulum attached near to the junction of the oesophagus and stomach that apparently stores nectar* while pollen grains are held in the main gut. The tail is prehensile and up to 11 cm long, while the body is up to 10 cm. Adult females are usually larger than males in weight, body length, tail length and snout length (Table 1). The species has no close relatives, being the sole representative of a monotypic superfamily (Kirsch, 1977). Wooller *et al.* (1981) have established that honey possums live for 12 months on average. They breed all year round, but show peaks in autumn, winter and spring when certain flowers are most abundant. Mark and recapture data indicate that most animals have a home range of less than a hectare (Wooller *et al.,* 1981). Females with young were especially sedentary in one south coastal study area, 80% of them being captured over several months in areas less than 50 m in diameter.

White-cheeked honeyeaters (Figure 1c) are common in woodlands and heaths in south-western Australia and on the east coast from Nowra in New South Wales to Cooktown in Queensland (Slater, 1974). They are a sleek bird 170-180 mm in length (Figure 1c), weighing 18 g on average. Bill (exposed culmen) lengths at Cheyne Beach ranged from 23-27 mm (Table 1). White-cheeked honeyeaters have predominantly black and white plumage, with flashes of yellow on the wings and edges of the tail. Unlike honey possums, honeyeaters do not eat pollen other than by accident (Paton, 1981); they forage only on nectar at flowers (Recher, 1977). Although the home ranges of white-cheeked honeyeaters were not documented in the study area, individual birds were seen flying between plants over distances in excess of 100 m on some occasions. However, most movements on feeding bouts occurred over lesser distances of 1-10 m, as has been documented in studies of honeyeaters elsewhere in south-western Australia (Hopper & Burbidge, 1978; Hopper & Moran, 1981).

MATERIALS AND METHODS

Observations of animals at flowers were undertaken during November 21-28, 1979 with Zeiss 10 x 40 binoculars either from a stationary vehicle or from chairs located 5-10 m away from the study plants. A single population of four *Banksia grandis* plants occurring within 0.1 ha on the south side of the uncleared Cheyne Beach townsite was studied. This population lies within the Appenteur Nature Reserve (W.A. Dept. Lands & Surveys reserve no. 36719, vested in the Western Australian Wildlife Authority). Six isolated clumps of *Eucalyptus angulosa,* each of 1-5 plants, were studied. The clumps were distributed along 0.3 km of track one kilometre SE of the townsite, on the SE corner of Appenteur Nature Reserve. The clumps of *E. angulosa* were observed sequentially each for five minutes during an observation period (both honeyeaters and honey possums were regularly observed feeding

*The fluid from the diverticulum of an animal killed while feeding on *Eucalyptus angulosa* flowers contained 9% sucrose equivalents on analysis with a pocket refractometer.

TABLE 1

Measurements made on plants and animals studied at Cheyne Beach

	Mean ± S.E.	Range	N
Banksia grandis			
No. flowers/inflorescence	4708 ± 735	3442 - 5892	4
Style length (mm)	33.5 ± 0.6	30.7 - 35.1	8
No. flowers/inflorescence			
opening at night	144 ± 17		16
opening during daylight	246 ± 22		16
Eucalyptus angulosa			
Diameter stamen array (mm)	38 ± 2	32 - 43	5
Maximum stamen length (mm)	14.8 ± 0.5	13 - 16	5
Style length (mm)	12.2 ± 0.4	11 - 13	5
Depth of floral cavity (mm)	6.2 ± 0.2	6 - 7	5
Honey possums			
Weight (g) male	7.8 ± 0.4	4.2 - 10.5	16
female	9.5 ± 1.0	5.4 - 13.3	10
Body Length (snout-vent; mm)			
male	76 ± 2	64 - 86	16
female	81 ± 2	71 - 91	11
Tail Length (mm)			
male	86 ± 2	72 - 99	16
female	90 ± 4	77 - 107	11
Snout Length (tip to eye; mm)			
male	12.5 ± 0.3	11 - 14	16
female	13.5 ± 0.4	12 - 15	11
White-cheeked honeyeaters			
Bill length (mm)	25.0 ± 0.3	23 - 27	17

within a minute of observation of each clump). The frequency of observation periods through hours of daylight and early evening is given in Figure 2e. For this study, a foraging bout was defined as observable feeding on one or more plants, terminated when the animal disappeared from view for longer than a minute, or when it ceased feeding and preened or engaged in other behaviour for longer than a minute. The time at which all foraging bouts occurred was recorded to ascertain whether diurnal variation in feeding existed. To compare feeding behaviours of honey possums and honeyeaters, the number of probes made on inflorescences or flowers was recorded and the duration of probes was timed with a stopwatch. Additionally, animals were carefully observed to record the frequency at which preening occurred and to note whether nectar or pollen or both were harvested.

The methods described by Hopper (1980) were used to trap honey possums, to mistnet honeyeaters, to harvest pollen onto vaselined microscope slides and to score the number of pollen grains on three 60 x 0.6 mm transects along each slide. To test whether pollen loads on honey possums were depleted by preening prior to sampling, a single animal was shot while feeding on *E. angulosa* and its pollen load was then compared with those from pit-trapped animals.

RESULTS

Banksia grandis

A total of 486 minutes (8.1 hours) was spent observing inflorescences of *B. grandis*—200 minutes in the morning, 104 in the afternoon and 182 in the early evening. During this time 21 foraging bouts by honey possums and 49 by white-cheeked honeyeaters were

observed (Figures 2a, b). Honey possums tended to avoid feeding in the middle of the day, favouring the early morning, late afternoon-early evening, and presumably, most of the night (cf. Vose, 1972). The honeyeaters fed sporadically throughout the day, with a peak of activity late in the afternoon through to dusk.

Data on feeding behaviours (Table 2) show that honeyeaters probed each inflorescence twice as many times as honey possums, that they took only a tenth of the time for each probe, and that they were never seen preening pollen from body surfaces between probes on the same inflorescence, whereas honey possums averaged 2.3 preens per inflorescence.

Fifteen of the 18 white-cheeked honeyeaters captured carried some *B. grandis* pollen, whereas only nine of the 34 honey possums examined carried pollen. Pollen loads sampled from the honeyeaters were two orders of magnitude greater than those from honey possums (Table 2).

TABLE 2

Statistics on feeding behaviour and pollen loads of honey possums and White-cheeked honeyeaters at Cheyne Beach

	Honey possums		White-cheeked honeyeaters	
	Mean ± S.E.	N	Mean ± S.E.	N
Banksia grandis				
No. probes/inflorescence	11 ± 3	7	24 ± 6	9
Probe duration (sec)	18.7 ± 1.9	13	2.5 ± 3	15
No. preens/inflorescence	2.3 ± 0.3	3	0	
Percent of animals carrying pollen	27	34	83	18
No. pollen grains/slide	0.3 ± 0.1	11	24.3 ± 11.1	16
Eucalyptus angulosa				
Feeding rate (sec/flower)	3.3 ± 0.3	49	2.5 ± 0.2	29
Percent of animals carrying pollen	64	11	94	16
No. pollen grains/slide	*15.1 ± 13.9	11	29.3 ± 9.0	16

*This figure includes data obtained from 10 animals caught in pit-traps plus one animal shot while feeding.

Eucalyptus angulosa

A total of 438 minutes (7.3 hours) was spent observing animals at flowers of *E. angulosa*—215 minutes in the morning, 128 in the afternoon and 95 in the early evening after sunset. The number of observed foraging bouts of honey possums was 44, while that for white-cheeked honeyeaters was 85. Honey possums avoided the heat of the day (1100–1500 hours), whereas white-cheeked honeyeaters fed throughout the whole day (Figures 2c, d).

Feeding rates on the eucalypt were only marginally faster for the honeyeaters. The birds probed only for nectar, whereas the honey possums were clearly seen licking pollen from anthers at least eight times, and probed for nectar on all foraging bouts.

Fifteen of the 16 white-cheeked honeyeaters carried *E. angulosa* pollen, while this applied to seven of the 11 honey possums. Pollen loads sampled from all honey possums were not significantly different from those of white-cheeked honeyeaters (Table 2). The mean pollen load for pit-trapped honey possums was 1.2 grains per sample, whereas that of the single animal shot while feeding was 154 grains.

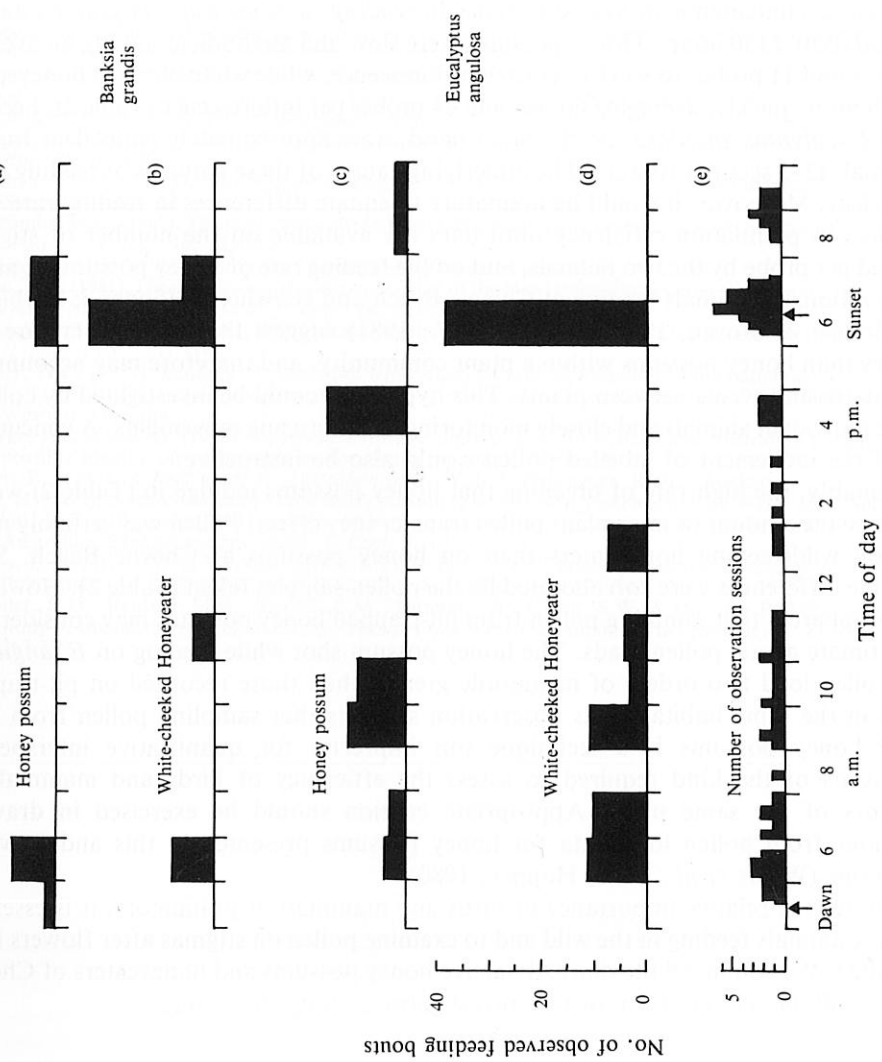

Figure 2. Frequency histograms of the number of observed foraging bouts of honey possums and white-cheeked honeyeaters on *Banksia grandis* **(a, b)** and *Eucalypitus angulosa* **(c, d).** The histogram in **(e)** shows the number of observation sessions completed at various times throughout daylight and early evening.

DISCUSSION

It is clear that detailed observations on feeding behaviour can be made on honey possums and honeyeaters at Cheyne Beach during daylight and crepuscular hours. These animals and the plants they feed on present an excellent opportunity to investigate the relative importance of birds and mammals as pollinators. Because of the short duration of field work in the present study, we were unable to acquire all the data necessary to satisfactorily address this question.

We have documented a striking difference in feeding rates on *Banksia grandis* during the period 0530–2130 hours. Honey possums were slow and methodical, taking an average of 206 secs and 11 probes to work over each inflorescence, while white-cheeked honeyeaters fed much more quickly, averaging 60 secs and 24 probes per inflorescence (Table 2). Feeding rates on *Eucalyptus angulosa,* on the other hand, were approximately equivalent for the two animals (2–3 secs per flower). The underlying causes of these patterns of feeding rates are not clear. Moreover, it would be premature to equate differences in feeding rate with differences in pollination efficiency until data are available on the number of stigmas pollinated per probe by the two animals, and on the feeding rate of honey possums at night.

Observations of animals feeding at Cheyne Beach and elsewhere (Hopper & Burbidge, 1978; Hopper & Moran, 1981; Wooller *et al.,* 1981) suggest that honeyeaters are less sedentary than honey possums within a plant community, and therefore may account for more outcrossing events between plants. This hypothesis could be investigated by colour-marking individual animals and closely monitoring their foraging movements. A concurrent study of the movement of labelled pollen would also be instructive.

Presumably, the high rate of preening that honey possums indulge in (Table 2) would also reduce the amount of inter-plant pollen transfer they effect. Pollen was certainly more visible on wild-feeding honeyeaters than on honey possums at Cheyne Beach. Such observable differences were corroborated by the pollen samples taken (Table 2). However, it is now apparent that sampling pollen from pit-trapped honey possums may considerably underestimate actual pollen loads. The honey possum shot while feeding on *E. angulosa* had a pollen load two orders of magnitude greater than those recorded on pit-trapped animals in the same habitat. This observation suggests that sampling pollen from live-trapped honey possums is a technique too imprecise for quantitative interspecific comparisons of the kind required to assess the efficiency of birds and mammals as pollinators of the same plant. Appropriate caution should be exercised in drawing conclusions from pollen load data for honey possums presented in this and previous publications (Wiens *et al.,* 1979; Hopper, 1980).

To resolve the relative importance of birds and mammals as pollinators, it is essential to observe animals feeding in the wild and to examine pollen on stigmas after flowers have been visited. We commend the diurnally-active honey possums and honeyeaters of Cheyne Beach as suitable material for further investigations along these lines.

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