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RELATIVE IMPORTANCE OF BIRDS AND MAMMALS AS POLLINATORS OF A BANKSIA AND A EUCALYPT

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ABSTRACT

Hopper, S.D. & Burbidge, A.A. (Western Australian Wildlife Research Centre, P.O. Box 51, Wanneroo, Western Australia 6065) 1981. Relative importance of birds and mammals as pollinators of a banksia and a eucalypt. Cunninghamia 1 :
Flowers of several banksias and eucalypts are now known to be visited by both birds and mammals seeking nectar and pollen. While it seems unlikely that many species of these genera are pollinated exclusively by either birds or mammals, quantitative differences may exist in the importance of these vertebrate groups as pollinators of particular species. The fortuitous discovery that honey possums (*Tarsipes rostratus*) feed in daylight as well as at night enabled a direct comparison of the feeding behaviour of these mammals with that of white-cheeked honeyeaters (*Phylidonyris nigra*) at Cheyne Beach on the south coast of Western Australia. The honeyeaters fed on *Banksia grandis* at a faster rate, they moved more rapidly between clumps of flowers, they preened less often, and they carried far greater pollen loads than did honey possums. Hence it is inferred that the honeyeaters were relatively more important as pollinators of this plant. In the case of *Eucalyptus angulosa*, the two animals appeared to be of equivalent importance as pollinators. For both plant species, the honeyeaters may have effected higher levels of outcrossing than did honey possums because of their greater mobility and local nomadism.

INTRODUCTION

As increasing attention has focused on vertebrate pollinators in Australia, it's become apparent that many plants attract both birds and mammals to their flowers (Morcombe 1968; Armstrong 1979; Ford et al. 1979; Turner 1981). 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 and 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, it may be possible to assess their relative importance by comparing the number of pollination events they effect per unit time (Primack and Silander 1975). To ~~obtain data on~~ this parameter, it would be necessary to observe and time animals picking up pollen and depositing it on stigmas. In practice, it is often difficult to do this, principally because microscopic inspection is required firstly to determine if stigmas are virgin, and secondly to count pollen grains deposited on stigmas of flowers by a vector. However, it is possible to infer the relative importance of vectors visiting the same flowers by (a) comparing the rates at which the flowers are visited, (b) comparing the effective pollen loads carried by the different vectors, and (c) comparing the behaviours adopted at flowers to determine the frequency of effective pollination events. We have adopted this inferential approach in the present study.

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 Michael Morcombe (1967, 1968). He rediscovered the rare and elusive 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, and appeared to feed without preference on, the dominant flowering species of Banksia, Adenanthos, Lambertia (Proteaceae), Beaufortia and Calothamnus (Myrtaceae).

Here, we present data from a follow-up study in November 1979 when we made the fortuitous discovery that honey possums feed in daylight under cool and cloudy conditions. 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. (Bull Banksia) is a small tree to 8m 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 (1-3m tall) but occurs as a scattered emergent in dense low heath (Fig. 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 31-35mm 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. Individual plants usually carried only one or two inflorescences in flower during the study period. No 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 such honeyeaters as red watttlebirds (Anthochaera carunculata), little wattlebirds (A. chrysoptera), New Holland honeyeaters (Phylidonyris novaehollandiae), western spinebills (Acanthorhynchus superciliosus) and yellow-throated miners

(Manorina flavigula) (Rooke 1979; Whelan and Burbidge 1980; Hopper and A.H. Burbidge unpubl.). No published observations on potential insect pollinators of B. grandis are available. At Cheyne Beach insect activity was limited to an occasional moth observed harvesting nectar soon after sunset.

Eucalyptus angulosa Schau. is a multi-stemmed mallee up to 5m tall of the south coastal regions of Western Australia and of South Australia (Chippendale 1973). It occurred in small isolated groves at Cheyne Beach emergent from dense low heath (Fig. 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 1.5-2.5cm long. Each flower is subtended by a short (4mm) pedicel. The deeply ribbed hypanthium is green and measures up to 1.5cm long. The style is short (11-13mm) and barely emergent from the orifice because the ovary roof is sunk deep (6-7mm) within the hypanthium. The orifice is c. 10mm in diameter at the rim. A flat-topped array of cream stamens splays up and outwards from the rim to a maximum diameter of 45mm. Individual stamens range in length from 16mm near the outside of the array to 4mm for those located on the inner side of the rim. Anthers are carried up to 8mm higher on the flower than the stigmatic tip of the style. Again no 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 small role in pollination, but their importance is minor in comparison to both birds and mammals observed at the study site.

Honey possums Tarsipes rostratus are small agile marsupials confined to south-western Australia, where they favour heath, scrub and open low woodlands on sandy soils. They weigh 7-20g when mature and have three distinctive stripes along the back (Fig. 1d). Adaptations to a diet of nectar and pollen include an elongated snout, highly reduced dentition, brush tongue and a thin-walled diverticulum attached to the stomach that apparently stores nectar and feeds it into the main gut where pollen grains germinate and are digested. The tail is prehensile and up to 11cm long, while the body is up to 10cm.

The species has no close relatives, being the sole representative of a monotypic superfamily. 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 50m in diameter.

White-cheeked honeyeaters (Phylidonyris niger) 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 170-180mm in length (Fig. 1c), weighing 18g on average. Bill lengths at Cheyne Beach ranged from 23-27mm. White-cheeked honeyeaters have predominantly black and white plumage, with flashes of yellow on the wings and edges of the tail. Unlike honey possums, these honeyeaters do not eat pollen - they forage only on nectar and insects at flowers (Paton 1981). 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 100m on some occasions. However, most movements on feeding bouts occurred over lesser distances of 1-10m, as has been documented in studies of honeyeaters elsewhere in south-western Australia (e.g. Hopper and Burbidge 1978; Hopper and Moran 1981).

MATERIALS AND METHODS

Observations of animals at flowers were undertaken during November 21-28 1979 with Zeiss 10x40 binoculars either from a stationary vehicle or from chairs located 5-10m away from the study plants. A single population of four Banksia grandis plants occurring within 0.1ha of land 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 0.3km 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. The frequency of observation periods through hours of daylight and early evening is given in Fig. 2. For this study, a foraging bout was defined as observable feeding 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 if 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, mistnet honeyeaters, harvest pollen onto vaselined microscope slides and score the number of pollen grains on three 60 x 0.6mm 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 (Fig. 2). 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 taken 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 on the honeyeaters were two orders of magnitude greater than those on honey possums (Table 2).

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 (11.00 - 15.00 hours), whereas white-cheeked honeyeaters fed throughout the whole day (Fig. 2).

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.

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. Pollen loads of all honey possums were not significantly different from those of white-cheeked honeyeaters (Table 2).

DISCUSSION

This study demonstrated significant differences in the feeding behaviour of honey possums and white-cheeked honeyeaters on Banksia grandis and Eucalyptus angulosa. On the banksia, white-cheeked honeyeaters were seen feeding twice as often as honey possums, they probed each inflorescence twice as many times, they took only a tenth of the time for each probe, and they preened far less frequently. Additionally, 83% of the honeyeaters and only 27% of the honey possums were found to be carrying B. grandis pollen, and the honeyeaters carried pollen loads two orders of magnitude greater than those of the honey possums. Even allowing that honey possums probably continue feeding through the night (Vose 1972) whereas white-cheeked honeyeaters don't, and that pollen loads on pit trapped honey possums are probably reduced by preening whereas those on immobilised honeyeaters in mist nets are not, it seems clear that white-cheeked honeyeaters accounted for far more pollination events than did the honey possums.

In the case of E. angulosa, feeding rates and pollen loads were similar for the two animals, and it can be inferred that they probably play equivalent roles as pollinators of this species.

At present, few data are available to assess whether the relative importance of pollinators documented at Cheyne Beach for the banksia and the eucalypt are representative of what occurs for each plant species throughout its geographical range. Indeed, the only relevant published study is that of Whelan and Burbidge (1980), who showed that honeyeaters regularly feed at inflorescences of B. grandis near Perth in a woodland habitat known to carry honey possum populations of much lower densities than those of the south coast (Davidge 1979). Hence birds are probably more important as pollinators than honey possums in this region as well.

If the Cheyne Beach data are representative of what occurs elsewhere, some interesting evolutionary questions need to be addressed in future work. Firstly, why are birds more important than mammals as pollinators of B. grandis? We suggest that a study of the plant's breeding system and patterns of pollen flow arising from pollinator foraging movements would be profitable to answer this question. At least two Western Australian banksias distantly related to B. grandis (i.e. B. menziesii and B. attenuata) appear to be obligate outbreeders (Scott 1980). If B. grandis has a similar breeding system, natural selection may well have favoured the attraction of those pollinators most likely to effect high levels of outcrossing. As discussed previously, honeyeaters appear to be less sedentary than honey possums within a plant community, and therefore may account for a higher number of outcrossing events. This hypothesis could be investigated by colour marking individual animals and closely monitoring their foraging movements. A study of the movement of labelled pollen would also be instructive in this regard.

The reasons why E. angulosa favours equivalent pollination from both birds and mammals constitutes a second question of considerable interest. Again, a study of this plant's breeding system is needed. All eucalypts investigated to date have proved to be facultative outcrossers, setting some self-pollinated seeds but with a majority of outcrossed seed (Moran and Griffin 1981). The flexibility of such a breeding system may confer a selective advantage on those plants that attract all available pollinators in a habitat, including both the sedentary mammals and the more mobile honeyeaters. Until the breeding system of E. angulosa has been elucidated and patterns of pollen flow arising from foraging movements of its pollinators are better understood, the significance of the present findings will clearly remain an open question.

Whatever the origins of the systems observed at Cheyne Beach, direct observations of the feeding behaviours of the honey possums and honeyeaters have allowed a quantitative assessment of their relative importance as pollinators to be completed. This places evolutionary hypotheses on a firm empirical base. Perhaps some of the current controversies concerning adaptations to bird and mammal pollination in Australian plants would resolve if observational data of the kind reported herein were acquired elsewhere in future studies.

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Table 1. Measurements made on plants and animals studied at Cheyne Beach

	mean $\pm$ S.E.	range	N
Banksia grandis			
No. flowers/inflorescence	4708 $\pm$ 735	3442-5892	4
Style length (mm)	33.5 $\pm$ 0.6	30.7-35.1	8
No. flowers/inflorescence opening at night	144 $\pm$ 17		16
No. flowers / inflorescence opening during daylight	246 $\pm$ 22		16
Eucalyptus angulosa			
Diameter stamen array (mm)	38 $\pm$ 2	32-43	5
Maximum stamen length (mm)	14.8 $\pm$ 0.5	13-16	5
Style length (mm)	12.2 $\pm$ 0.4	11-13	5
Depth of floral cavity (mm)	6.2 $\pm$ 0.2	6-7	5
Honey Possums			
Weight (g) male	7.8 $\pm$ 0.4	4.2-10.5	16
female	9.5 $\pm$ 1.0	5.4-13.3	10

Table 1. cont'd...

	mean$\pm$S.E.	range	N
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
<u>White-cheeked Honeyeaters</u>			
Bill length (mm)	25.0 ± 0.3	23-27	17

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$\pm$S.E.(N)	mean$\pm$S.E.(N)
BANKSIA GRANDIS		
No. probes/inflorescence	11$\pm$3 (7)	24$\pm$6 (9)
Probe duration(s)	18.7$\pm$1.9 (13)	2.5$\pm$3 (15)
No. preens/inflorescence	2.3$\pm$0.3 (3)	0
Percent of animals carrying pollen (N)	27% (34)	83% (18)
No. pollen grains/slide	0.3$\pm$0.1 (11)	24.3$\pm$11.1 (16)
EUCALYPTUS ANGULOSA		
Feeding rate (s/flower)	3.3$\pm$0.3 (49)	2.5$\pm$0.2 (29)
Percent of animals carrying pollen (N)	64% (11)	94% (16)
No. pollen grains/slide	15.1$\pm$13.9 (11)	29.3$\pm$9.0 (16)

FIGURE LEGENDS

Figure 1. Photographs of plants and animals studied at Cheyne Beach

(a) Stunted *Banksia grandis* tree 2m tall, emergent from dense low coastal heath (photographed in February after flowering had finished).

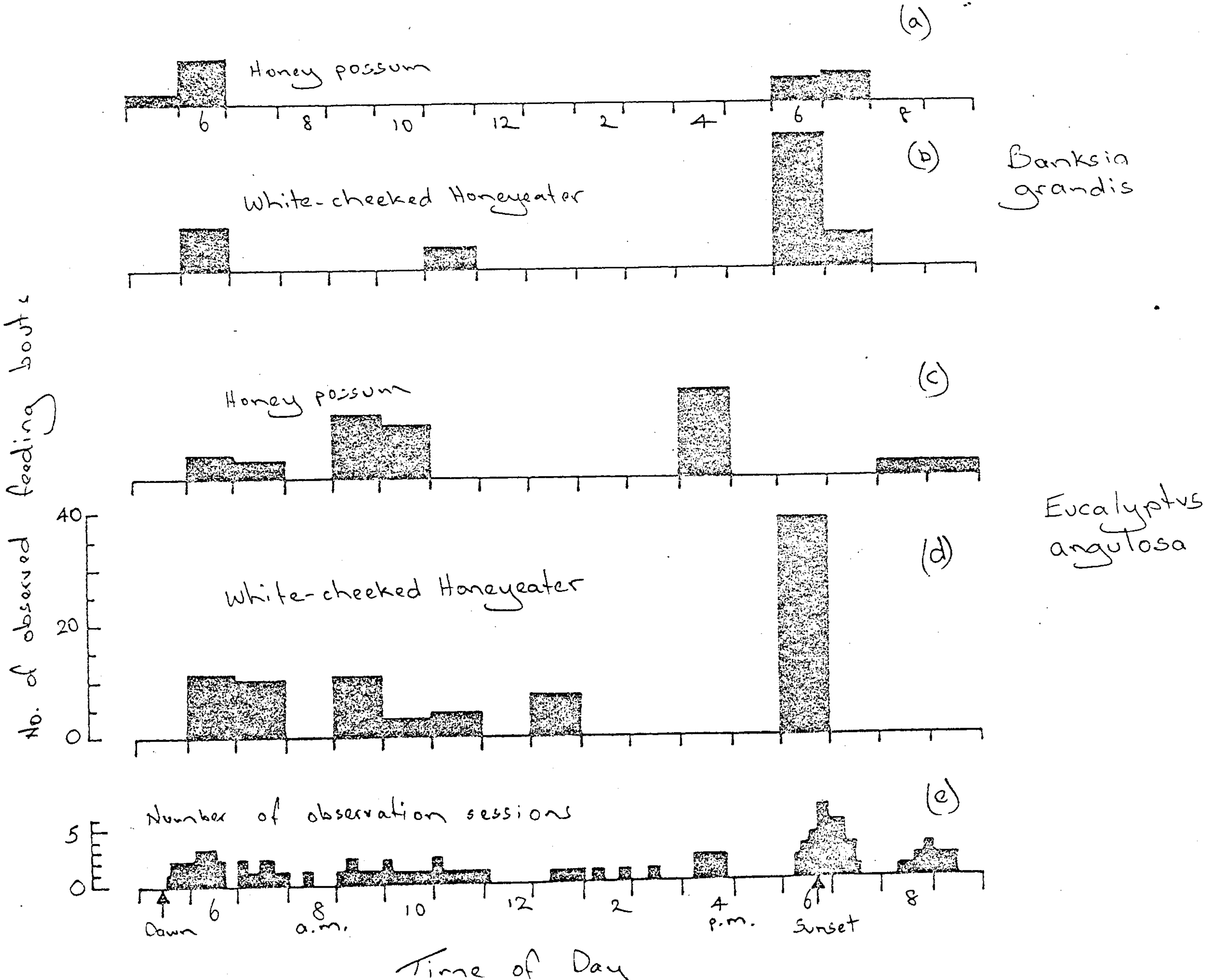
(b) Three isolated clumps of *Eucalyptus angulosa* 2-3m tall, emergent from dense low heath. A mistnet used to capture honeyeaters for pollen sampling is to the right of the *E. angulosa* in the foreground.

(c) White-cheeked honeyeater feeding on nectar of *Banksia baxteri*, an important food plant in autumn at Cheyne Beach.

(d) Honey possum on large cylindrical inflorescence of *Banksia grandis*.

(e) Honeypossum feeding on nectar of *Eucalyptus angulosa*.

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



(a)
Honey possum
6
8
10
12
2
4
6
8
(b)
White-cheeked Honeyeater
Banksia grandis
(c)
Honey possum
(d)
White-cheeked Honeyeater
Eucalyptus angulosa
No. of observed feeding bouts
0
20
40
(e)
Number of observation sessions
0
5
Dawn
a.m.
p.m.
Sunset
Time of Day

Fig 2