Differences in Pollinator Effectiveness of Birds and Insects Visiting Banksia menziesii (Proteaceae)

Author(s): M. W. Ramsey

Source: *Oecologia*, Vol. 76, No. 1 (1988), pp. 119-124
Published by: Springer in cooperation with International Association for Ecology
Stable URL: http://www.jstor.org/stable/4218644
Accessed: 28-06-2016 15:58 UTC

Oecologia (1988) 76:119–124

Oecologia

Differences in pollinator effectiveness of birds and insects visiting *Banksia menziesii* (Proteaceae)

M.W. Ramsey
Biological Sciences, Murdoch University, Murdoch, Western Australia 6150

Summary. The effectiveness of nectarivorous birds, introduced honey bees and staphylinid beetles as pollinators of *Banksia menziesii* was assessed. Staphylinids removed substantial amounts of pollen but did not deposit any onto stigmata. Abundance of beetles on inflorescences was related to the mean number of florets opening per day. Honey bees collecting pollen were more likely to effect pollination than those collecting nectar which only contacted stigmata when arriving or leaving an inflorescence. Nectar-foraging birds probed between florets 10.2 ± 0.8 ($\pm$SE) times, contacting 8–16 stigmata during each probe. Bees visited inflorescences ten times more frequently than birds although they deposited only 25% of the pollen that birds did on stigmata. Fruit set was ten times greater on inflorescences visited by birds than on inflorescences visited by bees. Bees were capable of removing as much pollen as birds but, because of direct pollen transfer to birds when florets opened during foraging, actual removal was probably much less. Selection for floret opening during nectar foraging by birds may have resulted from pollen removal by non-pollinating animals, such as staphylinids.

Key words: Pollination – Pollinator effectiveness – Nectarivorous birds – Honey bees – *Banksia*

Flowers of many plant species are visited by a variety of animals, although all may not be equally important to the reproductive success of the plants they visit (Primack and Silander 1975; Bertin 1982; Morse and Fritz 1983; Spears 1983; Lindsey 1984; Schemske and Horvitz 1984; Montalvo and Ackerman 1986; Sugden 1986). The most effective pollinators of a plant species will be those animals whose floral visitation results in the greatest reproductive success (Stebbins 1970).

Other pollinators contribute less to reproductive success by limiting the quantity or quality of compatible pollen loads to stigmata (Primack and Silander 1975; Bertin 1982). The deposition of pollen of lower quality may fertilise and pre-empt available ovules that are later aborted or produce inferior progeny (Stephenson 1981; Willson and Burley 1983; Wiens et al. 1987). Similarly, interspecific or self-incompatible pollen may clog stigmata, preventing the germination of later arriving pollen (Waser 1978; Shore and Barrett 1984). The removal of pollen by non-pollinating visitors or less effective pollinators decreases the amount of pollen available for reproduction (Schemske and Horvitz 1984). Similarly, the removal of floral nectar may affect pollen availability by altering the foraging behaviours of more effective pollinators (McDade and Kinsman 1980).

Most studies that have examined fruit set on plants visited by nectarivorous birds and insects (predominantly bees), have found that more fruit was produced when birds visited flowers (Carpenter 1976; Waser 1978, 1979; Bertin 1982; Collins and Spice 1986). In the genus *Banksia* (Proteaceae), flowering inflorescences are visited by birds, small mammals and insects, although their copious nectar production and large stigma to nectary distances suggest pollination by vertebrates (Paton and Turner 1985). Several studies have examined fruit set due to different floral visitors and found birds and insects equally effective (Whelan and Burbidge 1980; Paton and Turner 1985). In contrast, other species developed lesser numbers of fruit or no fruit at all when visited only by insects (Whelan and Burbidge 1980; Collins and Spice 1986). However, in these latter studies the reasons for the lower fruit set were not fully explored.

The present study examined the effectiveness of the major floral visitors of *Banksia menziesii* R.Br. as pollinators. These were staphylinid beetles (Coleoptera: Staphylinidae), introduced honey bees *Apis mellifera* and nectarivorous birds (honeyeaters, Meliphagidae). Other floral visitors either did not contact the reproductive structures or were too rare to be of consequence to fruit set. Specifically, I investigated the rates of visitation to inflorescences and how they foraged at inflorescences. In order to quantify pollinator effectiveness, pollen removal, pollen deposition and fruit set in response to visitation by these three groups were determined. The ways in which the different groups of visitors may influence, or potentially influence, the reproductive success of *B. menziesii* were also discussed.

Study species and field site

Banksia menziesii is a tree or woody shrub found near the west coast of south-western Australia (George 1981). About 600–1400 pink to red sessile florets (37–71 mm long) are arranged orthogonally around a central woody axis, forming inflorescences 4–12 cm long (George 1981; Ramsey 1986). Just prior to floret opening, pollen is deposited from sessile anthers onto the modified style-end, the pollen presenter, directly below the terminal stigmatic groove. After floret opening the style protrudes beyond the relaxed perianth (George 1981). Floret opening on inflorescences pro-

ceeds acropetally, with 30–70 opening per 24 h. Of these, approximately 95% open during the daytime, mostly in response to foraging by nectarivorous birds. By dusk, all of the pollen has been removed from florets suggesting nocturnal pollination is unlikely (Ramsey 1986, 1987a). Fruits of banksias are dry, dehiscent follicles formed from a single ovary containing two ovules (George 1981).

A field site of low, open woodland (4–6 m high) with *Banksia menziesii* and *B. attenuata* R.Br. as co-dominants was established within a reserve, 25 km south of Perth, Western Australia. *Banksia menziesii* trees are self-incompatible at this site (Scott 1980; Ramsey 1986). Flowering, during the 1986 study period occurred from March to September.

Methods

Visitation rates and foraging behaviour

The visits of honeyeaters to 25 inflorescences, and of honey bees to 6 inflorescences, were monitored over 3 days in June during separate, hourly, 10 min census periods from 0700 h to 1700 h. Temperatures were also recorded hourly to determine if they were related to the abundance of visitors.

Staphylinid beetles, 2–3 mm in length, resided on inflorescences. Thus their visits to inflorescences could not be determined. Instead, the numbers of individuals on inflorescences in 6 different stages of floret opening (shown below) were assessed:

na	No florets open
0 –1/4	Up to one quarter of florets open
1/4–1/2	One quarter to one half of florets open
1/2–3/4	One half of three-quarters of florets open
3/4–F	Three-quarters or more florets open
F	All florets open

Ten inflorescences in each stage were removed from trees, sprayed with insecticide, sealed in plastic bags and returned to the laboratory, where their florets were removed and the numbers of staphylinids counted.

The number of florets opening per 24 h were counted on 8 inflorescences during the floral stages to determine if staphylinid abundance was related to pollen availability.

Pollen removal

Pollen removal by the different visitor groups was assessed using differential exclosures. Fifteen inflorescences, each with one quarter to one half of its florets open, were assigned to the following four treatments:

(a) Open: Access to all visitors (6 inflorescences)
(b) Caged: Access to insects; birds excluded (3 inflorescences)
(c) Bagged: Access to staphylinids; honeyeaters and honey bees excluded (3 inflorescences)
(d) Bagged with insecticide: All floral visitors excluded (3 inflorescences)

Cylindrical cages constructed of semi-rigid plastic mesh (20 cm high × 14 cm diameter with 1 cm × 1 cm apertures) were placed on inflorescences and secured on the supporting stems. Fabric netting bags (1 mm × 1 mm apertures) were placed over the cages in the bagged treatments and tied at the bottom to restrict access to insects.

Ten florets per inflorescence were opened with a fine needle between 0600 h and 0700 h; surrounding florets were removed. Insecticide was sprayed on inflorescences of the total exclusion treatment. Cages and bags were then placed on inflorescences.

Twelve newly opened florets were sampled for pollen at 0700 h using separate 2 mm^3 cubes of glycerine jelly impregnated with basic fuchsin stain (Wooller et al. 1983). Pollen grains readily adhered to the cubes and all visible pollen on the florets was removed. After sampling, the cubes were stored separately in labelled plastic vials.

Thereafter, at 2 hourly intervals until 1700 h, 2 predetermined florets on the inflorescences were sampled for pollen. Bags were removed while sampling and replaced when finished. Florets were removed after sampling.

In the laboratory, cubes were placed on microscope slides with coverslips resting on top. Slides were warmed over a flame until the gel melted. All of the pollen grains on each slide were counted at X100 magnification.

Pollen deposition

Thirty inflorescences, each with almost half of its florets open, were assigned randomly to either open, caged or bagged treatments. Previously opened florets were removed. Treatments were left in place for 7 days, after which 10 florets from each inflorescence were selected. Bagging did not appear to affect the staphylinids as large numbers were found on inflorescences after the bags were removed.

The top 0.5 cm of each style was removed and placed in a drop of basic fuchsin stain. Under X50 magnification the tip at each style was cut along the stigmatic groove with a fine scalpel blade. The numbers of pollen grains within the stigmatic cavities were counted under X100 magnification. The scalpel blade was checked for pollen grains and rinsed after each sample. Pollen grains stained darker than the stigmatic and stylar tissues and were readily distinguished.

Fruit set

Forty-five inflorescences, each with florets fully formed but not yet opened, were selected on 19 trees. Trees were assigned to either open, caged or bagged treatments such that there were 15 inflorescences per treatment. Not all inflorescences on *B. menziesii* trees develop fruit (Whelan and Burbidge 1980), so that the number treated on each tree was less than the number that produced fruit the previous year; the remaining inflorescences were removed. This removal was likely to ensure the availability of nutrient resources for developing seeds on treated inflorescences. Similarly, it prevented the selective development of offspring on non-treated inflorescences which might have received higher quality pollen (Stephenson 1981; Willson and Burley 1983). Treatments were completed in April and left in place until September when inflorescences were harvested and the numbers of fruits determined.

Results

Effects of treatments

An assumption when using different exclusion treatments is that the behaviour of the floral visitors is not altered (Paton and Turner 1985). Bagging did not adversely influ-

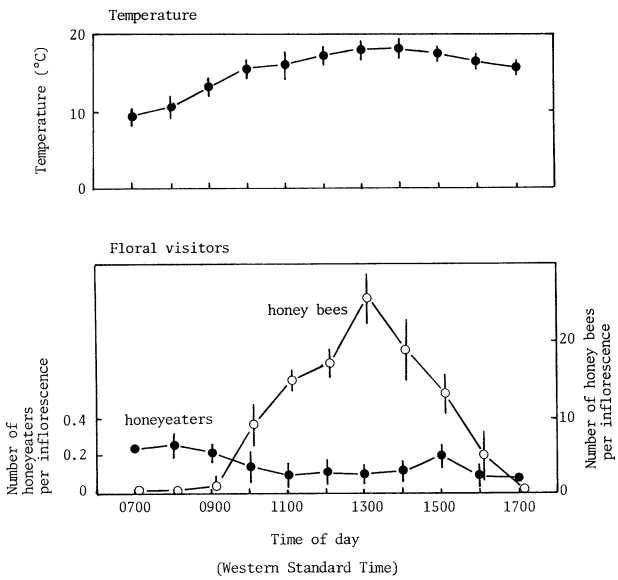

Fig. 1. Mean (±SE) numbers of visits by honeyeaters and honey bees to *Banksia menziesii* inflorescences. Visits were recorded over 3 days. Ambient air temperatures are shown at the top

ence fruit development, as inflorescences that were hand pollinated and bagged produced fruit (Ramsey 1986).

The effect of cages on the foraging behaviour of honey bees was examined recording the number and duration of visits to 3 caged and 3 open inflorescences. Open inflorescences received slightly more visits over a 10 min period ($x \pm$SE; open, 7.3 ± 0.9; caged, 6.0 ± 1.2) although these differences were not significant (Student's $t = 0.94$; df = 4, $P > 0.2$). Bees, however, tended to forage longer at caged inflorescences (open, 4.1 ± 0.3 min; caged, 5.0 ± 0.7 min) although not significantly so (Student's $t = 1.41$, df = 98, $P > 0.1$). The foraging behaviour of staphylinids within bagged inflorescences could not be assessed.

During all experiments, observations were made to ensure that inflorescences were visited and that exclosures restricted access to the appropriate group of floral visitors. Although open inflorescences allowed access to all floral visitors, differences between this treatment and the others reflect visitation by honeyeaters. Similarly, comparisons between caged and bagged inflorescences reflect differences between honey bees and staphylinids.

Visitation rates and foraging behaviour

Inflorescences received many more visits by honey bees than by honeyeaters (Fig. 1). The visitation rate was estimated as 104 visits per inflorescence per day for honey bees and as 10 visits per inflorescence per day by honeyeaters. Honey bee visitation occurred from 0900 h to 1600 h and was significantly correlated with ambient air temperature (Pearson product moment correlation; $r_p = +0.79$, df = 31, $P < 0.001$) with peak rates from 1200 h to 1400 h (Fig. 1). Honeyeaters visited inflorescences throughout the day although especially during the early morning (0700–0900 h) and late afternoon (1500–1700 h). The number of visits per inflorescence was inversely related to hourly temperature ($r_p = -0.56$, df = 31, $P < 0.001$). There were few visits before 0700 h.

The foraging behaviours of the most common species of honeyeaters (Western Spinebill *Acanthorhynchus superciliosus*, Brown Honeyeater *Lichmera indistincta*, New Holland Honeyeater *Phylidonyris novaehollandiae* and Little Wattlebird *Anthochaera chrysoptera*) were similar and their data have therefore been combined. However, the narrower bills and smaller heads of the Western Spinebills may result in less pollen being removed and deposited by this species (Ramsey 1987b). Honeyeaters landed on unopened florets at the distal end of an inflorescence and leaned forward to probe between the most recently opened florets. Simulating this action with preserved honeyeaters, it was estimated that the stigmata of 8–16 florets were contacted during each probe. A foraging bout lasted on average for 22.5 ± 1.8 s and consisted of 10.2 ± 0.8 probes (means ± SE for 417 observations).

The foraging behaviour of 94 bees was monitored, 84 collecting nectar and 10 collecting pollen. Foraging for pollen occurred mainly in the morning and, as most observations were conducted around midday, the number recorded as engaged in this activity was an underestimate. The average duration of a visit to an inflorescence by a bee foraging for nectar was estimated as 258 ± 18 s, although this was also an underestimate as 11% of individuals spent longer than 10 min at an inflorescence. In contrast, individuals foraging for pollen spent much less time at inflorescences (36.6 ± 11.0 s).

Bees collecting nectar rarely contacted stigmata except when arriving at, and departing from, inflorescences. They landed on the most recently opened florets contacting several stigmata, then burrowed between the open florets to reach the nectaries. When moving within an inflorescence, bees would push between florets below the stigmata. When departing, bees would climb onto florets, again contacting stigmata, and fly away. In contrast, bees collecting pollen contacted stigmata more often. They would land on inflorescences, as previously described, then walk around the inflorescence on the most recently opened florets collecting available pollen.

Staphylinid beetles were observed frequently removing pollen from florets. When florets were opened manually, they climbed up florets and removed pollen. If disturbed, or when all pollen was gone, they returned to the base of the florets. Staphylinids were not observed flying between inflorescences. All staphylinids found on inflorescences appeared to belong to the same species. The mean numbers of individuals per inflorescence ranged from 0.1 ± 0.1 to 32.8 ± 5.7, dependent on the floral stage of the inflorescence (Fig. 2; $X^2 = 34.01$, df = 5, $P < 0.001$, Kruskal-Wallis test). Abundance was significantly related to the mean number of florets opening per 24 h during each floral stage (Fig. 2; $r_p = +0.86$, df = 4, $P < 0.05$). As pollen availability is dependent upon the numbers of florets that open each day, staphylinid abundance may well be related to pollen availability. Alternatively, abundance may be related to nectar availability, if a greater number of florets opening per day results in greater nectar production.

Pollen removal

A significant amount of pollen was lost from florets on inflorescences where all visitors were excluded (bagged and insecticide) between 0700 h and 1700 h (Fig. 3; $P < 0.01$, Wilcoxon two-sample test), although pollen removal was

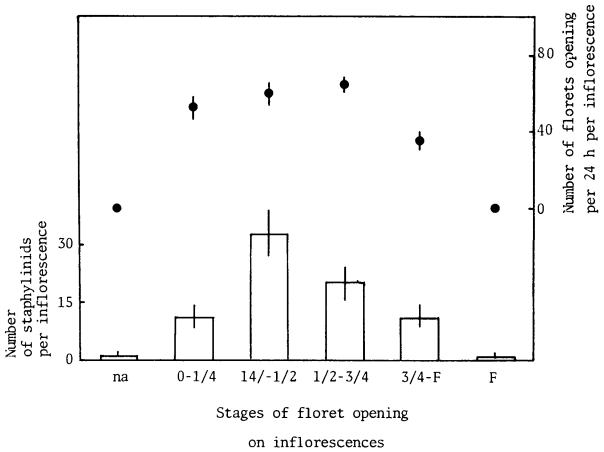

Fig. 2. Abundance of staphylinid beetles (Staphylinidae) and the numbers of florets opening per 24 h on *Banksia menziesii* inflorescences at different stages of floret opening (as defined in text). Mean (±SE) of 10 inflorescences for staphylinids and of 8 inflorescences for floret opening

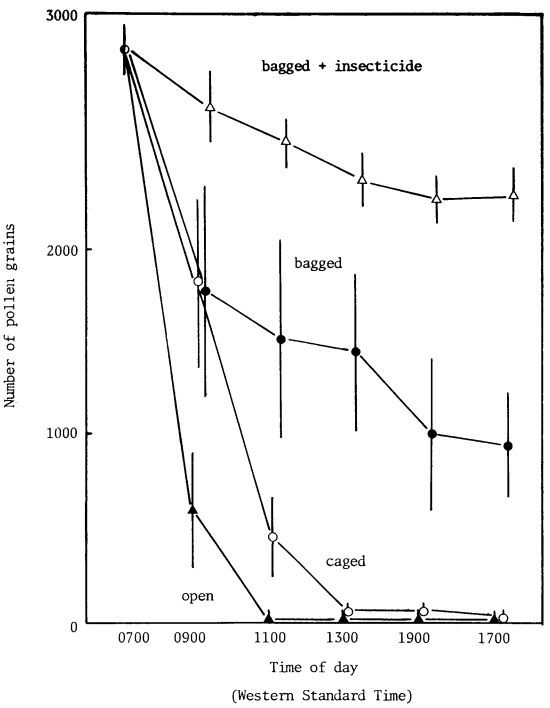

Fig. 3. Number of pollen grains remaining on individual *Banksia menziesii* florets with restricted access to different floral visitors. Means (±SE) of 12 florets from open inflorescences and of 6 florets for other treatments. The floral visitors excluded by each treatment are described in the text

greater when visitors had access. Staphylinids removed significantly more pollen than was lost from total-exclusion inflorescences by 1700 h ($P<0.005$) although the amount of pollen they removed was significantly less than that removed by either honey bees ($P<0.01$) or honeyeaters ($P<0.001$).

Within 4 h of presentation, virtually all of the pollen had been removed from florets on caged inflorescences (Fig. 3). As honey bees were not active before 0900 h (Fig. 1), pollen removal from the caged inflorescences between 0700 h and 0800 h was due to staphylinids. Thereafter, however, pollen removed from caged inflorescences was

Table 1. Number of *Banksia menziesii* stigmata from open, caged and bagged inflorescences containing pollen grains ($N=100$). The deposition of two or more grains was dependent upon treatment (3×2 test of independence)

Number of pollen grains within stigmata	Treatment		
	Open	Caged	Bagged
One or more	68	25	4
Two or more	38	9	0
Less than two	62	91	100
	$X^2=59.69$, df$=2$, $P<0.001$		

Table 2. Number of open, caged and bagged *Banksia menziesii* inflorescences producing fruit. Fruit production was dependent upon treatment (3×2 test of independence)

	Treatment		
	Open	Caged	Bagged
Fruit present	13	6	0
Fruit absent	2	9	15
	$X^2=23.14$, df$=2$, $P<0.001$		

rapid compared to that from bagged ones and was due to honey bees. Two hours after presentation, significantly more pollen had been removed from the open than the bagged or caged inflorescences ($P<0.05$), due to visitation by honeyeaters. By 1300 h similar amounts of pollen had been removed from both open and caged inflorescences ($P>0.5$).

Pollen deposition

Pollen deposition was low in all the treatments. The mean numbers of grains deposited on stigmata of florets on open, caged and bagged inflorescences were 1.27 ± 0.12, 0.35 ± 0.01 and 0.07 ± 0.02 respectively ($N=100$ for each treatment). More than twice as many florets from open inflorescences contained pollen grains than those from caged inflorescences (68% and 25% respectively). Only 4% of bagged florets contained pollen grains (Table 1).

Fruits of *B. menziesii* contain 2 seed wings (Scott 1982; Ramsey 1986), suggesting that both ovules must be fertilised before development of a fruit proceeds. Thus, the results have been analysed in terms of the number of florets containing 2 or more pollen grains, or less than this (Table 1).

The deposition of two or more pollen grains within stigmata was dependent upon treatment (Table 1). None of the florets from the bagged inflorescences (staphylinid access only) contained two or more pollen grains. Of the caged and open inflorescences, 9% and 38% of florets respectively contained two or more grains. Pairwise comparison (2×2 test of independence; Zar 1974) between bagged and caged treatments showed this to be a significant difference ($X^2=7.46$, df$=1$, $P<0.01$), as was that between caged and open treatments ($X^2=21.80$, df$=1$, $P<0.001$).

Fruit set

Fruit production on open, caged and bagged inflorescences was highly dependent upon treatment (Table 2). Of the

open inflorescences, 87% set fruit while only 40% set fruit on the caged inflorescences. None of the bagged inflorescences produced fruit. Pairwise comparison between open and caged inflorescences revealed this as a significant difference ($X^2 = 7.03$, df = 1, $P < 0.01$). In addition, open inflorescences produced 5.3 ± 0.7 fruits per inflorescence, significantly more than the 1.2 ± 0.5 produced on caged inflorescences (Student's $t = 45.1$, df = 28, $P < 0.001$).

Discussion

Nectar-feeding birds were the most effective pollinators of the self-incompatible *Banksia menziesii*, which concurs with previous studies of other bird-visited plants (Carpenter 1976; Waser 1978, 1979; Bertin 1982; Collins and Spice 1986). Despite a tenfold difference in visitation rates between honey bees and honeyeaters, birds deposited four times as much pollen as bees, resulting in approximately ten times greater fruit set. Similarly, hummingbirds deposited ten times more pollen than honey bees or bumble bees on stigmata of flowers of the self-incompatible *Campsis radicans* (Bignoniaceae) resulting in greater fruit set (Bertin 1982).

Free (1966) reported that honey bees pollinated a higher proportion of apple flowers when collecting pollen than when collecting nectar. Likewise, pollen collecting bees may be more effective pollinators of *B. menziesii*. Pollen collectors contacted greater numbers of pollen presenters and stigmata while foraging, thus increasing non-corbiculae pollen loads (Ramsey 1986) and the likelihood of pollen deposition. Also, as only a few florets have pollen on at any one time, these bees may have to visit a greater number of inflorescences while foraging, increasing the probability of transferring outcross pollen.

Overall, however, pollen deposition on stigmata by honey bees was low, although it was much greater than the resulting fruit set on comparable caged inflorescences. Assuming that pollen was deposited similarly on stigmata over whole inflorescences, the low fruit set may have been a consequence of the deposition of self-incompatible pollen. It is unlikely, however, that the deposition of self-pollen by honey bees would depress fruit set on open inflorescences by clogging stigmata (Shore and Barrett 1984) or pre-empting ovules (Willson and Burley 1983) as almost 92% of stigmata had no pollen deposited on them.

Pollen deposition on inflorescences visited by honeyeaters also exceeded fruit set. However, the levels of fruit set were much greater than those effected by bees and were similar to those reported in previous studies in similar areas (Whelan and Burbidge 1980; Scott 1982; Cowling et al. 1987). These results suggest that the maximal number of fruits per inflorescence was limited by factors other than the deposition of compatible pollen. The most likely factor is the availability of mineral nutrients (e.g. McCall and Primack 1987). If more ovules are fertilised than can be matured, selective abortion may retain only those fruits that are of high genetic quality (e.g. Willson and Burley 1983). Pollination of *B. menziesii* by honeyeaters may result in higher quality offspring, thus increasing female reproductive success.

Honey bees removed as much *B. menziesii* pollen as honeyeaters, suggesting a possible adverse affect on male reproductive success due to a reduction of pollen available for transfer by birds. Under natural conditions, however, florets open mainly in response to nectar-foraging by honeyeaters (Ramsey 1987a), resulting in up to half of the pollen of florets being transferred directly to the birds. Also, immediately after the departure of a bird from an inflorescence, staphylinids climb from the base of newly-opened florets and remove much of the remaining pollen. Thus, the impact of honey bees may not be as great as suggested by the pollen removal experiment of this study.

Pollen removal by flower-visiting staphylinid beetles has been reported previously, although pollination details were not given (Gottsberger 1985). During the study reported here, pollen removal by staphylinids was substantial although the amount deposited on stigmata was insufficient to initiate fruit set. As removal of pollen by non-pollinating floral visitors decreases male reproductive success (Schemske and Horvitz 1984), selection should favour floral traits minimising those pollen losses. Floret opening in *B. menziesii* after honeyeater visitation, if heritable, may have arisen in response to pollen removal by staphylinids or other non-pollinating animals. The direct transfer of pollen onto birds would decrease potential losses and increase the probability of deposition onto stigmata. Other selective forces, however, may also have been important, for instance in increasing outcrossing distance when reproductive success is related to pollen flow distances (Schemske 1983).

Although not universal, mechanical stimulation of floret opening has been noted for several other species of banksia, but whether opening occurs in response to nectar-seeking birds remaining to be determined (McFarland 1985). Flower opening caused by nectarivorous birds has been also reported for some species of Loranthaceae from Java and Central Africa although its significance remains unexplained (Docters von Leeuwen 1954; Feehan 1985). For several insect-pollinated plants, in which pollen serves as the primary attractant, flower opening in response to pollinator visitation has been interpreted as a mechanism to ensure the availability of pollen for plant reproduction (Faegri and van der Pijl 1979).

Honey bees have been introduced to Australia only since 1826 and their influence on the native fauna and flora is largely unknown (Pyke and Balzer 1985). The results of the present study suggest that honey bees are not directly affecting the reproductive success of *B. menziesii*. However, bees may affect reproductive success indirectly by removing nectar, which could alter the foraging behaviour of the honeyeaters.

Of the total 24 h nectar production of *B. menziesii* inflorescences, 32% is produced during the daytime (Newland 1982) and is thus available to honey bees. The greater nighttime nectar production may be completely utilised by honeyeaters at dawn before bees are active as Paton (1979) found for *Grevillea aquifolium* (Proteaceae), *Callistemon macropunctatus* (Myrtaceae) and *Amyena pendulum* (Loranthaceae). However, when honey bees removed a large proportion of the nectar produced during the day in these species, the feeding territories of New Holland Honeyeaters increased in size (numbers of flowers defended).

The visitation by birds of more flowers on different plants may increase pollination, in terms of both the quantity and quality of pollen deposited (McDade and Kinsman 1980). Although it would be unlikely that fruit set would increase in *B. menziesii*, the genetic quality of progeny may. In contrast, if nectar resources were reduced to levels that were insufficient to sustain avian pollinators, a decrease

in reproductive success would follow. This effect has been reported by McDade and Kinsman (1980) for populations of *Aphelandra golfodulcensis* and *Justicia aurea* (Acanthaceae). Both species are pollinated by larger Hermit Hummingbirds although nectar is also removed by other bird species and insects. Thus, although nectarivorous birds are the most effective pollinators of *B. menziesii*, further research is warranted on the future potential impact of the honey bee on the reproductive success of this species and other species that are visited by both birds and bees.

Acknowledgements. My thanks to Professor S.D. Bradshaw and Pauline and Brian Clay for allowing me to use the Harry Waring Marsupial Reserve. Dr R.D. Wooller and G.V. Vaughton kindly provided comments on earlier drafts of this paper.

References

Bertin RI (1982) Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans*, Bignoniaceae). Amer J Bot 69:122–134

Carpenter FL (1976) Plant-pollinator interactions in Hawaii: Pollination energetics of *Metrosideros collina* (Myrtaceae). Ecology 57:1125–1144

Collins BG, Spice J (1986) Honeyeaters and the pollination biology of *Banksia prionotes* (Proteaceae). Aust J Bot 34:175–185

Cowling RM, Lamont BB, Pierce SM (1987) Seed bank dynamics of four co-occurring *Banksia* species. J Ecol 75:289–302

Docters van Leeuwen WM (1954) On the biology of some Javanese Loranthaceae and the role birds play in their life-history. Beaufortia 4:102–207

Faegri K, van der Pijl L (1979) The principles of pollination ecology. 3rd ed. Pergamon Press, Oxford

Feehan J (1985) Explosive flower opening in ornithophily: a study of pollination mechanisms in some central African Loranthaceae. Bot J Linn Soc 90:129–144

Free JB (1966) The pollinating efficiency of honey bee visits to apple flowers. J Hort Sci 41:91–94

George AS (1981) The genus *Banksia* L.f. (Proteaceae). Nuytsia 3:239–473

Gottsberger G (1985) Floral ecology, report on the years 1981(79) to 1985. Progress in Botany 47:384–417

Lindsey AH (1984) Reproductive biology of Apiaceae. 1. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. Amer J Bot 71:375–387

McCall C, Primack RB (1987) Resources limit the fecundity of three woodland herbs. Oecologia (Berlin) 71:431–435

McDade LA, Kinsman S (1980) The impact of floral parasitism in two neotropical hummingbird pollinated plant species. Evolution 34:944–958

McFarland DC (1985) Flowering biology and phenology of *Banksia integrifolia* and *B. spinulosa* (Proteaceae) in New England National Park, N.S.W. Aust J Bot 33:705–714

Montalvo AM, Ackerman JD (1986) Relative pollinator effectiveness and evolution of floral traits in *Spathiphyllum friedrichathalii* (Araceae). Amer J Bot 73:1665–1676

Morse DH, Fritz RS (1983) Contributions of diurnal and nocturnal insects to the pollination of common milkweed (*Asclepias syriaca* L.) in a pollen-limited system. Oecologia (Berlin) 60:190–197

Newland CE (1982) The effect of changes in nectar availability on an assemblage of honeyeaters in a *Banksia* woodland, near Perth. BSc Hons Thesis, Murdoch University, Perth

Paton DC (1979) The behaviour and feeding ecology of the New Holland Honeyeater *Phylidonyris novaehollandiae* in Victoria. PhD Thesis, Monash University, Melbourne

Paton DC, Turner V (1985) Pollination of *Banksia ericifolia* Smith: Birds, mammals and insects as pollen vectors. Aust J Bot 33:271–286

Primack RB, Silander JA Jr (1975) Measuring the relative importance of different pollinators to plants. Nature 255:142–144

Pyke G, Balzer L (1985) Effects of the introduced honey-bee on Australian native bees. National Parks Wildlife Service, Occasional Paper No. 7

Ramsey MW (1986) Aspects of the anthecology of *Banksia menziesii*. R.Br. and *Banksia littoralis* R.Br. (Proteaceae) in relation to fruit-set. BSc Hons Thesis, Murdoch University, Perth

Ramsey MW (1987a) Floret opening in *Banksia menziesii* R.Br.; the importance of nectarivorous birds. Aust J Bot 36 (in press)

Ramsey MW (1987b) The seasonal abundance and foraging behaviour of honeyeaters and their potential role in the pollination of *Banksia menziesii*. Aust J Ecol (submitted)

Schemske DW (1983) Limits to specialization and coevolution in plant-animal mutualisms. In: Nitecki MH (ed) Coevolution. University of Chicago Press, Chicago, pp 67–109

Schemske DW, Horvitz CC (1984) Variation among floral visitors in pollination ability: a precondition for mutualism specialization. Science 225:519–521

Scott JK (1980) Estimation of the outcrossing rate for *Banksia attenuata* R.Br. and *Banksia menziesii* R.Br. (Proteaceae). Aust J Bot 28:53–59

Scott JK (1982) The impact of destructive insects on reproduction in six species of *Banksia* L.f. (Proteaceae). Aust J Zool 30:901–921

Shore JS, Barrett SCH (1984) The effect of pollination intensity and incompatible pollen on seed set in *Turnera ulmifolia* (Turneraceae). Can J Bot 62:1298–1303

Spears EE Jr (1983) A direct measure of pollinator effectiveness. Oecologia (Berlin) 57:196–199

Stebbins GL (1970) Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. Ann Rev Ecol Syst 1:307–326

Stephenson AG (1981) Flower and fruit abortion: Proximate causes and ultimate functions. Ann Rev Ecol Syst 12:253–259

Sugden EA (1986) Anthecology and pollinator efficacy of *Styrax officinale* subsp. *Redivivum* (Styracaceae). Am J Bot 73:919–930

Waser NM (1978) Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59:934–944

Waser NM (1979) Pollinator availability as a determinant of flowering time in Ocotillo (*Fouquieria splendens*). Oecologia (Berlin) 39:107–121

Whelan RJ, Burbidge AH (1980) Flowering phenology, seed set, and bird pollination of five Western Australian *Banksia* species. Aust J Ecol 5:1–7

Wiens D, Calvin CL, Wilson CA, Davern CI, Frank D, Seavey SR (1987) Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia (Berlin) 71:501–509

Willson MF, Burley N (1983) Mate choice in plants: tactics, mechanisms and consequences. Princeton University Press, Princeton

Wooller RD, Russell EM, Renfree MB (1983) A technique for sampling pollen carried by vertebrates. Aust Wildl Res 10:433–434

Zar JH (1974) Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, NJ

Received November 12, 1987