Impact of Commercial Honeybees on Flora and Fauna

In Ngarkat Conservation Park

A report for the Rural Industries Research and Development Corporation

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Foreword

Conservation, forestry and land management agencies in Australia are continually reassessing their policies on beekeeping in reserves with the risk that commercial apiarists may be excluded from reserves that they have traditionally used, leading to flow-on negative impacts on other horticultural industries.

The aim of this study was to assess the use of Ngarkat Conservation Park (a major South Australian reserve) by commercially-managed honeybees, establishing the magnitude of any impact on native flora and fauna and then, if there was an impact, determining if that impact was permanent or reversible and/or if there were ways of minimising any impact that would then allow commercial beekeepers to still have access without damaging the natural environment in a permanent sense.

The report, the latest addition to our diverse range of over 250 research publications, forms part of our Honeybee R&D program, which aims to improve the productivity and profitability of the Australian beekeeping industry.

Most of our publications are available for viewing, downloading or purchasing online through our website at www.rirdc.gov.au/pub/cat/contents.html

Peter Core
Managing Director
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Executive Summary

Honeybees Apis *mellifera* harvest nectar and pollen from a wide variety of Australian plants and can consume more than 80% of the nectar and or pollen being produced by some of the plants. This consumption of floral resources can reduce the abundance of endemic floral visitors and disrupt the pollination of native plants.

Conservation, forestry and land management agencies in Australia are continually reassessing their policies on beekeeping in reserves with the risk that commercial apiarists may be excluded from reserves that they have traditionally used. Loss of access to the floral resources of these reserves has been contested by beekeepers on the grounds that there has been inadequate assessment of the impact of honeybees on natural systems in Australia and inadequate assessment of the role of feral versus managed honeybees in any detrimental impact on the environment.

The aim of this study was to assess the use of Ngarkat Conservation Park (a major South Australian reserve) by commercially-managed honeybees, establishing the magnitude of any impact on native flora and fauna and then, if there was an impact, determining if that impact was permanent or reversible and/or if there were ways of minimising any impact that would then allow commercial beekeepers to still have access without damaging the natural environment in a permanent sense. These latter options were to consider management actions like resting sites in alternate years or setting limits on the sizes and length of tenure for any apiaries put in the park.

The original experimental design consisted of establishing a series of 15 sites in the central and northern regions of Ngarkat Conservation Park in areas where there had been no history of commercial use and negligible densities of feral colonies. The intention was to introduce commercial loads of honeybees to some sites and not others and measure the responses of native flora and fauna to these manipulations.

Despite this balanced design and insurance, an extensive fire burnt 1,600 km^2 of the park in December 1990 and burnt 14 of the 18 original sites. An additional 11 sites were established in 1991 but a drought during autumn 1991 reduced floral densities such that no sites were deemed suitable for stocking with honeybees by the beekeepers assisting with the project. The three year program of experimental manipulations recommenced in 1992. In 1992 five sites received commercial loads of honeybees and in 1993 nine sites received commercial loads of honeybees. The tenth site could not be stocked with honeybees in 1993 because of the condition of the access track to the site. All sites were re-examined in 1994 when no honeybees were placed on any of the sites.

In conjunction with these experimental manipulations a routine sampling program was conducted (i) to measure population sizes or densities of native flower-visiting birds, mammals and insects, (ii) to document patterns to the availability of floral resources, and (iii) to score seed production for the major plant species -*Banksia ornata,* in the presence and absence of commercial loads of honeybees.

Floral resources and animal activity were measured simultaneously at three sites (2 control (no honeybees) and 1 experimental (with honeybees) site or 2 experimental and 1 control site)

at the same distances and times on any one day, and measurements were repeated at least three times at each site during the winter period when honeybees were present at Ngarkat Conservation Park.

This study revealed that in each of three years when commercial loads of honeybees were placed in Ngarkat Conservation Park the quantity of pollen and nectar available to floral visitors declined at least in close proximity (a few 100 m) to apiaries. Despite depressing nectar resources, there were still substantial quantities of nectar (0.37 to 1.65 g of sugar/inflorescence) left unexploited on inflorescences at the end of the day.

Given the quantities of nectar left unexploited at inflorescences no native nectar-feeding animals should be affected by the presence of commercial loads of honeybees. The same can probably be said for pollen-harvesting animals but not with the same degree of confidence since the pollen requirements of the native fauna are not known.

Given the availability of food even at sites with honeybees there is no reason to expect the numbers of honeyeaters, small native mammals, or invertebrates to decline following the introduction of honeybees to sites. Counts of these animals and or their faeces revealed that there were no consistent differences in their abundances at sites with and without honeybees nor with distance from the apiary.

The only consistent response to the presence of honeybees in Ngarkat Conservation Park was an increase in seed production in areas stocked with honeybees. Some ecologists would argue that this enhanced seed production is nevertheless an impact that should not occur. However, for a mature die species like *Banksia ornata* that lives in fire prone areas and only reproduces via seeds there should be strong selective pressure on the plants to produce as many seeds as possible.

Although the presence of honeybees enhances seed production this does not infer that honeybees are better pollinators of *Banksia ornata* than native animals. The poor performance of native animals in this system is due to insufficient numbers of these animals visiting inflorescences rather than ineffectual pollination when flowers are visited.

The above results and conclusions that honeybees have no detrimental impact on the flora and fauna of *Banksia ornata* heathlands should not be blindly extrapolated to other areas. All that has been demonstrated is that there is no detrimental effect of honeybees on the flora and fauna of *Banksia ornata* heathlands of Ngarkat Conservation Park during the 2-3 month period when *Banksia ornata* blooms and in those years when floral densities exceed 4,000 inflorescences per hectare and/or nectar production is at least 320g/ha/day. Any extrapolation outside these dates or to other systems should be done with extreme caution until similar assessments have been made. This study however has developed simple techniques that could be used to quickly score floral resource production and consumption for other species of *Banksia* and other species of plant.

Introduction

Honeybees Apis *mellifera* were first introduced to Australia in the 1820s and both feral and managed colonies of honeybees are now widespread in Australia (Paton 1996). These introduced bees harvest nectar and pollen from a wide variety of Australian plants and can consume more than 80% of the nectar and or pollen being produced by some of the plants (Paton 1990,1993,1996). This consumption of floral resources can reduce the abundance of endemic floral visitors and disrupt the pollination of native plants (Pyke 1990, Paton 1993, 1996). Although only a few studies have been conducted to date those studies have lead to conclusions that the continued presence of honeybees in nature reserves conflicts with the primary purpose of those reserves - the conservation of endemic biota. There are also concerns that feral colonies of honeybees may displace native fauna from tree hollows although there has been inadequate assessment (Paton 1996). Conservation, forestry and land management agencies in Australia are continually reassessing their policies on beekeeping in reserves with the risk that commercial apiarists may be excluded from reserves that they have traditionally used. Loss of access to the floral resources of these reserves has been contested by beekeepers on the grounds that there has been inadequate assessment of the impact of honeybees on natural systems in Australia and inadequate assessment of the role of feral versus managed honeybees in any detrimental impact on the environment.

In South Australia the major reserve used by beekeepers is Ngarkat Conservation Park in the South-East of South Australia (Fig. 1) where there are extensive areas of *Banksia ornata* heathlands. Ngarkat Conservation Park is part of a large 270,000 ha reserve system that includes Mt Shaugh Conservation Park, Mt Rescue Conservation Park and Scorpion Springs Conservation Park. These other reserves abut Ngarkat Conservation Park. Most of the 208 registered bee sites are located in the western and southern third of this reserve system and beekeepers place up to 120 hives on these sites during winter to exploit the floral resources of *Banksia ornata.* Sites are stocked with honeybees usually from late May until late July or early August when many of the beekeepers shift their hives to other areas including almond orchards where they have pollination contracts. Not all bee sites are stocked with honeybees in any one year.

Beekeepers argue that access to this reserve in particular is crucial if they are to continue to provide adequate pollination services to almond crops. Without access to the floral resources being produced by *Banksia ornata* in this reserve their hives would not be able to maintain adequate strength to be fully effective as pollinators of almonds. Excluding beekeepers from this reserve could clearly impact other important horticultural industries.

The aim of this study was to assess the use of Ngarkat Conservation Park by commercially-managed honeybees, establishing the magnitude of any impact on native flora and fauna and then, if there was an impact, determining if that impact was permanent or reversible and/or if there were ways of minimising any impact that would then allow commercial beekeepers to still have access without damaging the natural environment in a permanent sense. These latter options were to consider management actions like resting sites in alternate years or setting limits on the sizes and length of tenure for any apiaries put in the park.

Methods

The original experimental design consisted of establishing a series of 15 sites in the central and northern regions of Ngarkat Conservation Park in areas where there had been no history of commercial use and negligible densities of feral colonies. The intention was to introduce commercial loads of honeybees to some sites and not others and measure the responses of native flora and fauna to these manipulations. These experimental manipulations needed to be conducted in areas where previous exposure to honeybees had been negligible to eliminate the possibility that past exposure to honeybees had already eliminated those taxa that were sensitive to honeybees. If the sensitive taxa had already been affected then additions of honeybees now would no longer induce a measurable response, or no further response. Fortunately the central regions of Ngarkat Conservation Park had not been used by commercial apiarists and the density of feral colonies was so low that honeybees could not be detected with usual baiting techniques (F. Lacey pers. comm.) -although we subsequently found about 1 feral colony per 20 sq km in the areas that we used. This was less than 0.001 feral colonies per hectare. A lack of water over summer and a dearth of suitable places for feral swarms probably accounted for the low density.

In the first year of the study 5 of the 15 sites were to be stocked with 40-100 hives while the other 10 remained free of honeybees. In the second year the five sites that were stocked with honeybees in the first year were to be restocked, and another 5 sites stocked for the first time leaving 5 sites still without honeybees. The intention with this design was to determine if there was a ‘gradual’ increase in the magnitude of the impact over 2 years compared with 1 year. In the third year none of the sites were to receive commercial loads of honeybees, the intention being to determine if any recovery would occur if sites were rested.

These experiments and measurements also needed to be performed at appropriate scales - both spatial and temporal- and adequately replicated at these scales to eliminate chance events influencing the outcomes of the results or their interpretation. For example control sites needed to be sufficiently distant from experimental sites to prevent the possibility of honeybees intruding onto control sites from the experimental sites. Appropriate spatial scales were determined from some initial work around several commercial apiaries in other parts of the Park in 1989. These observations revealed that honeybees moved out distances of about 1.5 km from an apiary in good weather during winter and shorter distances in inclement weather, with the level of resource use being most intense within 500 m of the apiary. Based on this, measurements at each site needed to consider documenting biotic resources and interactions with honeybees over distances of up to 1.5 km from a central point. Each site, therefore consisted of the area enclosed within a 1.5 km radius of a central point and central points of adjacent sites were at least 3 km away from each other to prevent intrusions of honeybees from experimental sites onto control sites. For temporal scales, we simply mimicked the times when commercial beekeepers used the reserve with commercial loads of honeybees (40-110 hives) being placed on selected sites from late May or early June through to late July or mid August.

In 1990, 18 sites were selected with the aid of beekeepers in *Banksia ornata* heathlands that were at least 13 years post-fire and supporting adequate densities of *Banksia ornata* to support commercial loads of honeybees. These 18 sites were then divided into groups of three adjacent sites and one of those sites chosen to receive a commercial load of honeybees. Five of these sets of sites received commercial loads of honeybees in the winter of 1990, the additional set of three sites were selected as an insurance against losing some sites to wildfires during the course of the three year study.

Despite this balanced design and insurance, an extensive fire burnt 1,600 km^2 of the park in December 1990 and burnt 14 of the 18 original sites. An additional 11 sites were established in 1991 but a drought during autumn 1991 reduced floral densities such that no sites were deemed suitable for stocking with honeybees by the beekeepers assisting with the project. The three year program of experimental manipulations recommenced in 1992. In 1992 five sites received commercial loads of honeybees and in 1993 nine sites received commercial loads of honeybees. The tenth site could not be stocked with honeybees in 1993 because of the condition of the access track to the site. All sites were re-examined in 1994 when no honeybees were placed on any of the sites.

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Floral resources and animal activity were measured simultaneously at three sites (2 control (no honeybees) and 1 experimental (with honeybees) site or 2 experimental and 1 control site) at the same distances and times on any one day, and measurements were repeated at least three times at each site during the winter period when honeybees were present at Ngarkat Conservation Park. Simultaneous measurements at three sites allowed possible differences in bird, mammal and insect activity and floral behaviour due to weather conditions to be accounted for in the assessments and, with repeated measurements, we could document the extent to which pollen and nectar resources and animal activity were being depressed at sites stocked and not stocked with honeybees throughout the flowering season of *Banksia ornata,* as well as documenting any patterns as a function of distance from an apiary.

To do this we established a series of four transects each 1.5 km long that radiated out from the central point of each site (Fig. 2). Each transect was tagged with coloured flagging tape with distances from the central point marked at 100 m intervals. Along each transect we measured plant densities and counted the numbers of inflorescences or cobs produced by *Banksia ornata* in 50 m x 4 m quadrats placed at 100 m intervals along each of the four transects. The quantities of pollen present at inflorescences was then estimated by counting the number of pollen presenters still fully laden with pollen on samples of 20-30 inflorescences at different distances along two of these transects. The numbers of fully laden pollen presenters on cobs were counted up to 100, but if there was more than 100, this was simply indicated as being in excess of 100 and not counted accurately to save time. Counts of insects feeding on nectar and pollen (honeybees, native bees and ants) were also made at each of these inflorescences.

Nectar availability at *Banksia ornata* inflorescences was measured by collecting samples of six flowering cobs in separate plastic bags from areas within 100 m of each central point and also at distances of about 1000 m from each central point (again along two of the transects) in the late afternoon after honeybee activity had ceased. These samples were then spun rapidly on a short piece of rope to centrifuge any nectar into the corner of the plastic bag. The volume of nectar was then measured with calibrated syringes or capillary tubes and the concentration of the sugar in the fluid measured with a refractometer. Volumes and concentrations were then converted to milligrams of sugar taking into account differences in the density of different concentrations. The numbers of invertebrates (staphylinid beetles, ants, flower spiders etc.) that were spun from the inflorescences were also counted.

The quantities of nectar and pollen produced by *Banksia ornata* inflorescences were determined at each site during the middle of the flowering season. For nectar production this involved covering 12 inflorescences with fine voile bags prior to anthesis. These bags prevented animals from accessing these inflorescences when they were flowering. Prior to covering the inflorescences an upside down 2 litre plastic drink bottle, with most of the sides and top removed, was placed around the inflorescence and wired in place such that any nectar dripping from the inflorescence would be collected in the upturned top, the lid allowing this fluid to be easily removed. Bagged inflorescences were then revisited every 2-4 days and the volume and concentration of nectar collecting in the drink bottle measured. At the end of flowering the inflorescence was removed, its length measured and then placed in a plastic bag and spun on a short piece of rope to remove the remaining nectar. The volume and concentration of this nectar was then measured as described above. The total quantity of nectar produced by each inflorescence (mg of sugar) during its floral life was then calculated.

Pollen production was measured from 10 inflorescences at each site by removing the fully-laden pollen presenters of five recently opened virgin flowers and placing these samples in separate tubes. The pollen on these presenters was then steeped in a known volume of lactophenol (0.4 ml) and the number of pollen grains in duplicate aliquots (0.9 μl) counted under a microscope with the aid of a haemocytometer and used to estimate the quantity of pollen presented by each flower.

The numbers of nectar-feeding birds (various species of honeyeater, including Tawny-crowned, Purple-gaped, New Holland, and White-fronted Honeyeaters) were censused along two of the four transects at each site by counting all the birds seen within 50 m of either side of the transect line. Bird counts commenced at the central point at 0830h and took 2 hours to complete, with observers travelling along the transect at a rate of 100 m per 4 minutes. The numbers of birds seen in each 100 m section of the transect were counted on the way out along the transect line and then those counts were repeated on the way back to the central point.

The abundances of small nocturnal flower-visiting mammals (mainly Silky Mice *Pseudomys apodemoides)* could not be counted directly. Instead their abundances were determined in two ways: from the numbers caught in pitfall traps set near the centre of each site; and, by the number of faeces left on top of inflorescences. Pitfalling consisted of erecting a 100 m long by 30 cm high flywire drift fence over 10 evenly-spaced pits, each pit being about 60 cm deep and 20 cm in diameter. Unsuspecting small mammals fell into the pits at night with the drift fence helping to direct them into the pits. Pitfalls were set for three consecutive nights and any small mammals that were caught were extracted at dawn, tagged and released. Both Silky Mice *(Pseudomys apodemoides)* and Pygmy Possums *(Cercartetus* spp.) often defaecate while sitting on top of *Banksia* inflorescences and these deposits were used to provide a second measure of abundance or activity. Faecal deposits on cobs were counted at the same time that inflorescences were scored for pollen availability.

Seed production by *Banksia ornata* inflorescences was measured by tagging samples of inflorescences at different times in the year and by subjecting them to different treatments. Small strips of coloured plastic flagging on which treatment details could be written were used to tag inflorescences. Most inflorescences were left alone once tagged to measure natural rates of seed production (sites without honeybees) or rates of seed production in the presence of honeybees (sites with hives). Rates of seed production were also measured at cobs where different-sized floral visitors had been excluded with different-sized mesh enclosures (hessian, bird-wire). Other inflorescences were exposed overnight (nocturnal animals having access) or during the day (diurnal animals having access) with these inflorescences being kept covered with fine hessian bags at other times. Other experiments included adding extra pollen to some cobs to determine if pollination rates limited seed production for *Banksia ornata*. If the plants were receiving adequate service from their pollinators, then adding extra cross pollen to flowers should not lead to an increase in seed production. If, however, pollinators were limiting then adding extra pollen to receptive stigmas should increase seed production compared with inflorescences that did not receive this extra pollen. In 1990, additional pollen was added to flowers on one occasion only but in subsequent years pollen was added to inflorescences every 3-4 days, with each inflorescences receiving additional pollen at least 3 times. Pollen from up to five other individual plants were used in these pollination experiments. The numbers of seeds produced at each inflorescence were then scored 6-9 months later, when follicles had matured sufficiently to be counted.

Activity patterns of honeybees, estimates of the quantities of nectar and pollen being harvested by hives, and changes in the strength and stored resources of hives were also recorded. This involved selecting 10 hives within an apiary and recording the numbers of bees returning to each hive every hour throughout the day. Return rates were determined using a stopwatch to record the time for 10 bees to return and enter the hive. When return rates were high (< 25 sec for 10 bees to return) this was repeated five times for each hive each hour. However, if return rates were low then the numbers of bees entering the hive was countered for up to 2 minutes. Following this the numbers of bees carrying and not carrying pollen, including the size and colour of the pollen load, was recorded for up to 50 returning honeybees at each hive on each hour. The sizes of pollen loads were estimated by eye as very large, large, medium, small and trace based on the extent to which the corbiculae were covered and the depth of the load. During the day samples of 20-40 honeybees that were returning to hives, and others that were departing from a hive, were collected and killed with gaseous ethyl acetate. The size and colour of the pollen loads were estimated on these dead bees and the hindlegs with the pollen loads removed and placed in vials. These were then steeped in lactophenol (1 ml) and the type of pollen and numbers of pollen grains present counted in small aliquots under a microscope with the aid of a haemocytometer. The total number of grains present could then be estimated. The potential quantity of nectar harvested by honeybees was determined by gently squashing each bee and collecting the fluid that was released. The volume of this fluid was measured with calibrated capillary tubes and its refractive index measured with a hand-held sugar refractometer. Differences in the quantity of fluid removed from honeybees that were departing from a hive versus those that had just returned was used to estimate the average quantity of nectar being harvested per trip. These data could then be combined with return rates to provide an estimate of the quantity of nectar and pollen being harvested by hives.

Changes in the condition and strength of hives during winter occupancy of Ngarkat Conservation Park were made by estimating the per cent of each side of each frame that contained eggs, brood, honey and pollen shortly after the arrival of hives in the park and then again shortly before their departure. The differences in the amounts of brood (including eggs), honey and pollen between these two periods was used to judge net performance.

Results

Annual variation in the production of floral resources by Banksia ornata.

The number of *Banksia ornata* inflorescences produced per hectare, the size of the inflorescences that were produced, the quantity of nectar produced per inflorescence and the quantity of pollen produced per flower varied from one year to the next (Table 1). Of these variables, the number of inflorescences produced per hectare was the most variable between years, and ranged from an average of 8,809 inflorescences/ha in 1992 to 597 inflorescences/ha in 1995 (Table 1). Numbers of inflorescences produced were significantly lower during drought conditions (1991, 1995) than in other years. Nectar and pollen production varied about 3 fold over a four year period (1990-93) with inflorescences producing between 719 and 2,003 mg sugar/cm of inflorescence and between 7,966 and 22,432 pollen grains per flower in any one year. Production of floral resources was lowest in the drought year of 1991, and in general variation in rates of pollen and nectar production reflected the annual variations m production of inflorescences (Table 1). In the drought year of 1991 not only were the numbers of inflorescences per hectare reduced, but the quantities of pollen and nectar produced by an inflorescence were also lower. The sizes of inflorescences also varied between years with smaller inflorescences being produced in drought years but inflorescence length was not as variable as other floral attributes (Table 1).

Influence of honeybees on the availability of nectar at Banksia ornata *inflorescences.*

The quantities of nectar present at inflorescences differed between years (Table 2) and varied seasonally in each of the four years when samples were taken throughout the flowering season (ANOVAs, $p < 0.001$, 0.006, < 0.001 and 0.003 for 1990, 1991, 1992 and 1993 respectively; Table 2). In most years the quantity of nectar found on *Banksia ornata* inflorescences declined through the flowering season. Given this, subsequent analyses of the influence of honeybees on the availability of nectar were made on sets of data collected during each month.

The quantities of nectar present close (100-300m) to and far (900-1000m) from the central points of sites not receiving honeybees did not differ significantly so these samples were pooled for analysis and presentation (Table 2). However, the quantities of nectar present at inflorescences taken close to an apiary often differed from the quantities found at inflorescences sampled further away and so those samples were kept separate. In fact, in each of the three years that honeybees were placed at sites, *Banksia ornata* inflorescences close (within 100-300m) to an apiary held lower quantities of nectar than inflorescences sampled at sites that were not stocked with honeybees. These differences were statistically significant in 1992 and 1993, but not in 1990 (Table 2). The quantities of nectar present at distances of around 1 km from an apiary were higher than those close to an apiary (although they were only significantly higher in 1993) and were similar to the quantities found at inflorescences at sites not stocked with honeybees, except in 1993. In 1993 the quantities of nectar present at 900-1000m from an apiary were significantly lower than the amounts found at sites not stocked with honeybees (Table 2) suggesting that in 1993 honeybees depressed nectar levels out to a distance of about 1 km from an apiary.

Despite significant reductions in the quantities of nectar present at inflorescences near apiaries the amounts remaining, however, were still substantial with averages ranging from 0.37 to

1.65 g of sugar per inflorescence during the periods when honeybees were present. These quantities were in fact higher than the quantities present at inflorescences in years of poorer flowering when no honeybees were placed on sites. In general the quantities of nectar present at inflorescences at sites without honeybees reflected annual differences in flowering, with levels lowest in drought years (1991, 1995) and highest in years of good flowering (eg. 1993, Table 2). In 1993 the quantities of nectar present at inflorescences at sites not stocked by honeybees were often above 2 grams of sugar per inflorescence.

Influence of honeybees on the availability of pollen at Banksia ornata *inflorescences.*

The quantities of pollen present at inflorescences varied seasonally and between years (Table 3, ANOVAs). In general, pollen availability at inflorescences was lower in years of poor flowering, and declined towards the end of the flowering season (Table 3). In years of above average flowering (eg 1990, 1992 and 1993) inflorescences at sites not stocked with honeybees often averaged in excess of 50 fully laden pollen presenters.

For sites not stocked with honeybees there were no significant differences in the quantity of pollen present at inflorescences sampled at different distances from the central point of those sites (ANOVAs, $p>0.05$) and so data for different distances for these sites were pooled for presentation and further analysis. At sites stocked with honeybees there were significant differences in the quantities of pollen (measured as numbers of fully laden pollen presenters) with distance from an apiary. At sites stocked with honeybees, the quantity of pollen present on inflorescences was consistently lower at close (<350m) and intermediate (350-700m) distances from an apiary than samples taken further away (800-1200m, >1200m) and also significantly lower than at sites not stocked with honeybees (ANOVAs, Tukey's tests, Table 3). Inflorescences close to apiaries often averaged less than 10 fully laden pollen presenters with the quantity of pollen present at inflorescences increasing progressively with distance away from apiaries. At distances of 800-1200m and 1200-1500m the numbers of fully laden pollen presenters were still usually much lower than the numbers found at sites without honeybees but the differences were not significant (Table 3).

Quantities of pollen and nectar harvested by hives of honeybees

Individual honeybees brought back varying amounts of nectar and/or pollen when they returned to their hives (Tables 4, 5). Nectar-collecting bees carried on average 27-36 μl of fluid when they returned to a hive. The concentration of this fluid however varied from 22-54% sugar (or equivalent) by weight, resulting in honeybees returning with 8-24 mg sugar. The primary factor influencing the quantities of sugar brought back to the hive was concentration which was usually lower following inclement, rainy weather. Given that honeybees departed hives with 6-9 μl of body fluid with a concentration of 10-15% sugar (or equivalent) by weight, the net quantity of sugar returned to the hive by nectar-gathering honeybees was about 15 mg per trip.

The quantities of nectar brought back by pollen-harvesting honeybees were often lower. In general the quantities of nectar brought back to the hive by pollen harvesting honeybees was lower when the bees carried larger pollen loads (Table 5). Honeybees returning with trace amounts of pollen returned with 10-16 mg sugar, those with large to very large pollen loads returned with around 4-5 mg sugar, and those carrying intermediate loads of pollen returned with 6-8 mg sugar (Table 5).

Large to very large pollen loads contained 580,000 to 925,000 *Banksia* pollen grains. Smaller loads were found to consist of progressively lower numbers of pollen grains (Table 5).

On a per hive basis there were on average 27,655 bee returns per day (range 10,615 to 58,558) in 1993 of which around 3,266 were pollen gathering honeybees (Table 6). Of the bees returning with pollen 71-97% (mean 86%) had collected *Banksia* pollen. Generally more honeybees returned with larger loads of *Banksia* pollen than they did when foraging on pollen from flowers of other plants. These other plants included *Eucalyptus* spp., *Baeckea crassifolia, Styphelia exarrhena* and *Allocasuarina meulleriana.* Based on the measured rates of return of honeybees with different loads, hives harvested on average 409 g sugar per day and 1,230 million *Banksia* pollen grains per day (Table 6).

Over the two month period that hives were placed on experimental sites in 1993 they showed a net increase in the amount brood present (equivalent to about 1.5 frames) and a net increase in the amount of honey stored (equivalent to about 6 frames, Table 7).

Influence of honeybees on the abundances of nectar-feeding birds (honeyeaters)

Fourteen species of honeyeater were detected during counts of birds along line transects. Nine species were recorded in most years and most sites. These were the Tawny-crowned Honeyeater *Phylidonyris melanops,* New Holland Honeyeater *P. novaehollandiae,* White-fronted Honeyeater *P. albifrons,* Purple-gaped Honeyeater *Lichenostomus cratitius,* White-eared Honeyeater *L. leucotis*, Yellow-plumed Honeyeater *L. ornatus*, Brown-headed Honeyeater *Melithreptus brevirostris,* Red Wattlebird *Anthochaera carunculata* and Spiny-cheeked Honeyeater *Acanthagenys rufogularis.* These species were widely but patchily distributed over Ngarkat Conservation Park with different species apparently responding to different habitat features (heaths with no emergent eucalypts versus mallee heath versus stringy-bark woodlands). The most abundant and widespread species was the Tawny-crowned Honeyeater. One or more individual White-naped Honeyeaters *Melithreptus lunatus,* Yellow-faced Honeyeaters *Lichenostomus chrysops*, Singing Honeyeaters *L. virescens*, Fuscous Honeyeaters *L. fuscus* and Yellow-throated Miners *Manorina flavigula* were recorded in one or more years (particularly 1994) at a few sites.

In assessing the responses of honeyeaters to influxes of commercial loads of honeybees, all species have been pooled and average densities (honeyeaters/ha) calculated for different sectors of the 1.5 km long transects. Although there were no seasonal changes in the numbers of honeyeaters recorded per hectare in 1990, 1991, 1992 and 1993 (ANOVA, $p = 0.22$, 0.64, 0.19 and 0.67 respectively) data have still be analysed on a monthly basis because of seasonal differences in resource availability (Tables 2, 3). Table 8, therefore, shows the monthly mean numbers of honeyeaters recorded at sites stocked and not stocked with honeybees that were censused in each month, as well as the numbers recorded at distances close (0-500m), intermediate (500-1000m) and far (1000-1500m) from apiaries.

In 1990, 1992 and 1993 the mean number of honeyeaters per hectare typically ranged between 2 and 3 honeyeaters per hectare for sites stocked and not stocked with honeybees and did not differ significantly. However, there were significant differences between other years in the numbers of honeyeaters recorded at sites (ANOVA, $p << 0.001$, Table 8) with the numbers recorded in 1994 (3.75 honeyeaters/ha) being significantly higher than in all other years, and the counts in 1995 (1.40 honeyeaters/ha) significantly lower than those counted in 1990, 1993 and 1994, but not significantly different from the numbers counted in 1991 and 1992 (Tukey's tests).

In the three years when honeybees were introduced to sites in Ngarkat Conservation Park there were no significant or systematic differences in the numbers of honeyeaters recorded at sites stocked and not stocked with honeybees and no systematic differences in the numbers of honeyeaters recorded with distance from an apiary in any one month (Table 8, ANOVAs, p's ranging from 0.43 to 0.78). If reductions of floral resources (nectar, Table 2) affected the numbers of honeyeaters using the *Banksia ornata* heathlands then that affect would be expected to be greatest close to an apiary where nectar resources were most depressed. The above analyses of variance revealed that there were no significant reductions in the numbers of honeyeaters recorded close to an apiary compared to further away and so no evidence that honeybees affected the numbers of honeyeaters using the *Banksia ornata* heathlands of Ngarkat Conservation Park.

Influence of honeybees on the numbers of small mammals using Banksia ornata *heathlands in Ngarkat Conservation Park*

Eight species of small mammal were trapped in pitfall lines set near the centre of each site. These included the Silky Mouse *Pseudomys apodemoides*, Little and Western Pygmy Possums *Cercatetus lepidus* and *C. concinnus*), Common and Fat-tailed Dunnarts *(Sminthopsis murina* and *S. crassicaudata*, Ningaui *(Ningaui yvonneae)*, Mitchell's Hopping Mouse (*Notomys mitchelli)* and the introduced House Mouse *Mus domesticus.* Of these only three species, the silky mouse and the two pygmy possums, used the floral resources of *Banksia ornata*. Table 9 shows the mean numbers of these mammals that were caught at sites stocked and not stocked with honeybees between 1990 and 1995. The numbers of mammals caught varied between years with numbers of silky mice and pygmy possums being greatly reduced in years of poor flowering (ie. 1991 and 1995, and to a lesser extent 1994). There were no significant differences between trapping rates at sites stocked and not stocked with honeybees (t-tests, p's > 0.05) except in August 1993 when significantly more silky mice were trapped at sites without honeybees. This result, however, is likely to reflect the vagaries of trapping, since trapping at four of the nine sites supporting honeybees in July 1993 and again in September 1993 showed much greater numbers than were trapped in August. At those four sites in July 1993 an average of 10.8 ± 1.9 silky mice were caught compared with 2.00 ± 0.7 in August 1993 and 9.8 ± 4.0 in September 1993.

The second method of assessing the abundances of small mammals involved recording the numbers of inflorescences carrying mammal scats. This method provides a second estimate of small mammal abundance or activity relative to the availability of flowers. When floral abundances were high less than 5% and often less than 3% of the inflorescences carried scats (Table 10). Only when floral abundances were low (1991, 1995) or declined towards the end of the flowering season (ie August in some years) did the per cent of inflorescences with faecal deposits approach 20% (Table 10). There were no consistent differences in per cent of inflorescences carrying scats with distance from an apiary or between sites stocked and not stocked with honeybees in those months when sufficient replicate sites were scored (Table 10, ANOVAs, p > 0.08). The only significant difference was found in May 1993 when a significantly higher proportion of inflorescences carried scats at the four sites stocked with honeybees compared with those had not been stocked with honeybees (p= 0.005).

Patterns of use of floral resources of Banksia ornata *by honeybees around apiaries*

The numbers of honeybees working the flowers of *Banksia ornata* were considerably higher when commercial apiaries had been placed at a site. In areas near to apiaries (<350m) the average number of honeybees recorded per 1000 inflorescences varied from 83 to 480 honeybees, but was usually between 200 and 300 honeybees/1000 inflorescences at least between 1030 and 1400h (Table 11). These numbers were significantly higher than the numbers of honeybees recorded at inflorescences not stocked by honeybees (Table 12). Control sites, however, were not entirely free of honeybees with small numbers of feral honeybees (0.3 to 22 per 1000 inflorescences) being detected at sites without apiaries (Table 11). In general the numbers of honeybees working flowers declined with distance from an apiary, but many of those differences with distance from an apiary were not significantly different (Tukey's tests). Large variances may have contributed to the inability to detect statistically significant reductions in honeybees at greater distances from an apiary. Observations on flight directions of individual honeybees arriving and departing from inflorescences revealed that at least some bees were travelling at least 1 km from an apiary to forage.

Influence of honeybees on the abundances of other invertebrates visiting Banksia ornata *inflorescences*

Various flies, native bees, wasps, ants and beetles were recorded at inflorescences of *Banksia ornata.* Of these, native bees and ants were the most frequently encountered during field observations, with both taxa primarily visiting inflorescences to harvest pollen. However, the numbers of native bees and ants visiting the flowers of *Banksia ornata* were relatively low in each of the three years m which honeybees were placed at sites in Ngarkat Conservation Park. In 1990 the maximum number of native bees recorded using inflorescences between 1030 and 1400h was around 5 native bees/1000 inflorescences, in 1992 up to 40 natives bees/1000 inflorescences were recorded, while in 1993 up to 10 native bees/1000 inflorescences were recorded (Table 12). At least three species of native bees were observed of which a species of *Leioproctus* was the most widely encountered. Statistical analyses revealed that there were no significant differences in the numbers of native bees recorded using *Banksia ornata* inflorescences with distance from an apiary or between sites stocked and not stocked with honeybees (Table 12).

Ants were more prominent at inflorescences than native bees with peak abundances of between 75 and 130 ants/1000 inflorescences being recorded in the years when honeybees were introduced to sites in Ngarkat (Table 13). As with native bees there were no statistically significant differences in the numbers of ants recorded using flowers at different distances from an apiary or between sites stocked and not stocked with honeybees (Table 13). In general the numbers of ants recorded harvesting floral resources from *Banksia ornata* inflorescences were much higher in 1991, 1994 and 1995 when there were fewer inflorescences. In these years there were 300-600 ants/1000 inflorescences.

Influence of honeybees on the production of seeds by Banksia ornata *in Ngarkat Conservation Park*

The presence of commercial loads of honeybees at a site resulted in an increase in the numbers of seeds produced per inflorescence by *Banksia ornata* in Ngarkat Conservation Park (Table 14). When honeybees were present at a site the average number of seeds produced per inflorescence ranged from 8.3 to 12.5 seeds/inflorescence. The average seed production at sites not stocked with honeybees in the same years ranged from 3.1 to 7.3 seeds/inflorescence, significantly lower than seed production at sites stocked with honeybees (Table 14).

Seed production at sites not stocked by honeybees was significantly enhanced with the addition of pollen to samples of inflorescences in 1990, 1992 and 1993, indicating that *Banksia ornata* in Ngarkat Conservation Park was pollinator limited in these years (Table 14). In the poorer flowering year of 1991 the addition of pollen to samples of inflorescences did not increase seed production, indicating that in this year visitation rates by native fauna were sufficient for the plant to set a full complement of seed. Seed production 1991 even with additional pollination was substantially lower than in the other years suggesting that drought conditions may restrict seed production in some years.

In 1992 and 1993 the addition of pollen every 3-4 days to inflorescences at sites not stocked with honeybees resulted in these inflorescences setting 9-11 seeds/inflorescence, comparable to the numbers of seeds set by inflorescences at sites with honeybees. In 1990, however, seed production by inflorescences receiving extra pollen at sites without honeybees only raised seed production to around 6 seeds/inflorescence and well below the average of 9 or more seeds/inflorescence set at sites stocked with honeybees. In this year, however, inflorescences were only given additional pollen on one occasion when only some of the flowers would have been receptive, so a slightly poorer response to additional pollination should be expected. In comparison the addition of pollen to inflorescences at sites with honeybees did not result in a significant increase in seed production in 1990 or 1992, suggesting that with the addition of honeybees the plants received adequate visitation from pollinators. The slight increase recorded at inflorescences that received additional pollination in 1993 was significant (t-test, $p = 0.012$, Table 14), suggesting that in some years even the presence of commercial loads of honeybees may not lead to full complements of seeds being set.

The number of seeds produced by *Banksia ornata* inflorescences tended to decline with distance from an apiary (Table 15). The numbers of seeds produced at 100m, 500m and 1000m from an apiary were significantly different to the quantities produced at locations and sites not stocked with honeybees in 1993 (p's <0.03) but the numbers set at 1500m were not significantly different to samples from areas without honeybees ($p = 0.09$). At this distance seed production could be significantly enhanced with the addition of pollen (t-test, $p = 0.02$), but at distances closer to an apiary additional pollination did not lead to a significant increase in seed production (t-tests, p's >0.05). These data suggest honeybees enhanced seed production out to a distance of about 1 km from an apiary.

Discussion

This study revealed that in each of three years when commercial loads of honeybees were placed in Ngarkat Conservation Park the quantity of pollen and nectar available to floral visitors declined at least in close proximity (a few 100 m) to apiaries. Despite depressing nectar resources, there were still substantial quantities of nectar (0.37 to 1.65 g of sugar/inflorescence) left unexploited on inflorescences at the end of the day. Given that most honeyeaters (eg Tawny-crowned, New Holland, Purple-gaped Honeyeaters) only need to harvest about 5g of sugar per day to satisfy their energy requirements (eg Paton 1982), honeyeaters are unlikely to be affected by the activities of honeybees in Ngarkat during the winter flowering season of *Banksia ornata.* Even in areas with honeybees, honeyeaters should still be able to collect their daily requirements of nectar easily even at the end of the day. Given this there should be no reductions in the densities of honeyeaters close to apiaries. Transect counts of honeyeaters confirmed this, with the densities of honeyeaters being similar at sites stocked and not stocked with honeybees. Furthermore, honeyeaters, particularly Tawny-crowned Honeyeaters, were often detected breeding within 50m of an apiary providing additional evidence that the presence of honeybees was not restricting the profitability of their foraging.

Similar arguments can be developed for the other fauna that visited *Banksia ornata* inflorescences in Ngarkat Conservation Park. Given the quantities of nectar left unexploited at inflorescences no native nectar-feeding animals should be affected by the presence of commercial loads of honeybees. The same can probably be said for pollen-harvesting animals but not with the same degree of confidence since the pollen requirements of the native fauna are not known. Close to an apiary inflorescences usually averaged around 10 fully-laden pollen presenters at any one time and this should be more than adequate to satisfy the requirements of individual animals (particularly given their low densities). Even when there are no fully laden pollen presenters, native fauna like native bees may still be able to readily access pollen by forcing buds to open. On several occasions when native bees landed on inflorescences with negligible pollen they mandibulated the tips of buds that were about to open, forcing the bud to open and in the process shedding pollen neatly on to the flower's pollen presenter. They then consumed this pollen before forcing another flower to open. A lack of fully-laden pollen presenters, therefore, may not affect native bees. In comparison, honeybees were not observed to force open buds when confronted with an inflorescences with little pollen. Instead they moved to another inflorescence.

Given the availability of food even at sites with honeybees there is no reason to expect the numbers of honeyeaters, small native mammals, or invertebrates to decline following the introduction of honeybees to sites. Counts of these animals and or their faeces revealed that there were no consistent differences in their abundances at sites with and without honeybees nor with distance from the apiary.

The only consistent response to the presence of honeybees in Ngarkat Conservation Park was an increase in seed production in areas stocked with honeybees. Some ecologists would argue that this enhanced seed production is nevertheless an impact that should not occur. However, for a mature die species like *Banksia ornata* that lives in fire prone areas and only reproduces via seeds there should be strong selective pressure on the plants to produce as many seeds as possible.

Although the presence of honeybees enhances seed production this does not infer that honeybees are better pollinators of *Banksia ornata* than native animals. The poor performance of native animals in this system is due to insufficient numbers of these animals visiting inflorescences rather than ineffectual pollination when flowers are visited.

As a consequence of inadequate numbers of native fauna, only a small proportion of the available inflorescences were visited frequently by them and so floral resources accumulated at inflorescences. Subsequently many inflorescences suffered reduced seed production because of inadequate pollination. Inadequate pollination was easily demonstrated by adding pollen to flowers by hand.

This apparent imbalance between native pollinators and *Banksia ornata* in the Ngarkat heathlands occurred in each of three years when honeybees were introduced to the area. However, in the drought year of 1991 when floral resources were reduced, surplus pollen and nectar was less obvious and seed production by the plants was not pollinator limited. Floral densities in this year were deemed by experienced beekeepers to be inadequate to support commercial apiaries. Based on statistics provided in Table 1, the quantity of nectar produced by *Banksia ornata* in Ngarkat Conservation Park was 8-fold lower in 1991 than in 1992.

The lack of surplus resources can be easily illustrated by reference to the quantities of floral resources being produced relative to those being harvested by individual hives. In 1991 approximately 4.1 kg sugar/ha was produced by *Banksia ornata* over the entire winter flowering season. Assuming the flowering season lasts about 100 days this is equivalent to about 41 g/ha/day. If individual hives harvested an average of 410 g/day (Table 6) then hives would need exclusive use of about 10 ha. An apiary of 100 hives would need at least 1,000 ha and honeybees would have to forage out to distances of at least 1.8 km from their hives. Given that bees rarely travelled more than 1 km from their hives even in good conditions during winter, apiaries placed on study sites in 1991 would have probably lost condition. In 1992 and 1993 considerably more nectar was produced per hectare with average production being around 320g/ha/day and 1. 11 kg/ha/day respectively. At these levels of production, an individual hive would need about a hectare of heathland habitat, and an apiary of 100 hives would only need to forage out to a distance of about 650m from the apiary. If the foraging was spread out over distances of 750m then within that region there would be substantial quantities available to native animals. For example in 1992 there would have been 15.5 kg of sugar produced per day that was not used by honeybees. This is equivalent to about 90g/ha/d, enough to support about 18 honeyeaters per hectare.

Several factors probably account for the general lack of nectar-feeding animals in the *Banksia ornata* heathlands of Ngarkat Conservation Park during winter. First cold temperatures greatly restricts the activity of many insects and so they are unlikely to be frequent and reliable floral visitors over winter. Second the numbers of honeyeaters and small mammals using *Banksia ornata* may be limited by the number that survive over summer and autumn. Ngarkat provides few floral resources for honeyeaters over summer and autumn so most honeyeaters probably leave this reserve during those times. The habitats that produce substantial quantities of nectar during summer and autumn in the southeast region of South Australia are in the more mesic coastal areas to the west and southwest of Ngarkat. Although not quantitatively documented there is a general increase in the numbers of honeyeaters in these coastal regions during summer and autumn, including Tawny-crowned Honeyeaters, New Holland Honeyeaters, Purple-gaped Honeyeaters, Red Wattlebirds and Spiny-cheeked Honeyeaters. These five species are amongst the most frequently counted m Ngarkat during winter. The more mesic coastal areas, however, have been extensively cleared for agriculture. Substantial areas of the drier sandy deserts (places like Ngarkat and the Big Desert Wilderness in adjacent Victoria), however, remain because these areas were least suited for agriculture. As a result of disproportionate clearing, little suitable summer habitat may remain in areas to the south and west of Ngarkat to support honeyeaters during summer and autumn and so population sizes of honeyeaters in the region as a whole may decline over summer and autumn. If so, then that could limit the numbers of birds that can subsequently recruit back into the drier heathlands of places like Ngarkat during winter and so lead to inadequate pollinator service for the plants of the area.

Other areas of *Banksia ornata* heathland closer to the coast support higher densities of honeyeaters with densities as high as 23 honeyeaters per hectare in some areas (Paton 1995). These areas actually produce less nectar per hectare than Ngarkat (Paton 1995) so clearly Ngarkat could support many more birds. Densities of around 20 honeyeaters per hectare (about an 8-10-fold increase on current densities of honeyeaters using Ngarkat) would probably have alleviated pollinator limitation to seed set in most years.

The above results and conclusions that honeybees have no detrimental impact on the flora and fauna of *Banksia ornata* heathlands should not be blindly extrapolated to other areas. All that has been demonstrated is that there is no detrimental effect of honeybees on the flora and fauna of *Banksia ornata* heathlands of Ngarkat Conservation Park during the 2-3 month period when *Banksia ornata* blooms and in those years when floral densities exceed 4,000 inflorescences per hectare and/or nectar production is at least 320g/ha/day. Any extrapolation outside these dates or to other systems should be done with extreme caution until similar assessments have been made. This study however has developed simple techniques that could be used to quickly score floral resource production and consumption for other species of *Banksia* and other species of plant.

In conclusion, in most winters there was surplus nectar being produced by *Banksia ornata* in Ngarkat Conservation Park and surplus pollen. The explanation for this was that there were insufficient native fauna present in the reserve to exploit all of the resources. Introductions of commercial loads of honeybees to sites in Ngarkat Conservation Park did not affect the numbers of honeyeaters, small mammals or invertebrates living in the reserve during winter but did result in a substantial increase in seed production for *Banksia ornata. Banksia ornata* reproduces after a fire only by seed, so excluding honeybees from this reserve during winter might be detrimental to the long term survival of this plant. The results of this study should be extrapolated cautiously to other systems but the techniques developed to assess the availability of floral resources may provide a basis for quickly assessing other areas particularly other Banksia heathlands.

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Figure 1 .
Map showing the location of Ngarkat Conservation Park in South Australia.

Figure 2.
Diagram illustrating the arrangement of plant quadrats along 1.5 km long transects radiating out from the central point of each site.

Only two of the four transects are shown in any details and only to a distance of 600m. 50m x 4m plant quadrats were placed at 100m intervals along each transect but in the figure are only shown at distances of 100m, 300m and 500m from the central point.

Table 1.
Annual variation in the numbers of inflorescences produced by *Banksia ornata* at 15-18 sites in Ngarkat Conservation Park, as well as annual variation in the size of inflorescences and in the quantities of nectar and pollen produced at these inflorescences.

In 1990, 18 sites were studied but 14 of these were burnt in December 1990 and were replaced with 11 new sites from 1991 onwards. Data for 1990, therefore, are not strictly comparable to data for the subsequent years, since different sites were involved. Information on the numbers of inflorescences produced are based on the numbers of inflorescences counted in up to sixty 50 m x 4 m quadrats positioned at 100 m intervals along four 1.5 km transects radiating out from each of the sites. Although not all quadrats were recounted each year, those that were recounted were used to calculate changes in floral production from one year to the next. The data given in the Table are the total number of inflorescences produced by *Banksia ornata* over the entire flowering season. The length of inflorescences is based on measurements of 120-240 inflorescences taken at each of the 15-18 sites between mid-July and mid-August. Standard errors for these measurements ranged from 0.12 to 0.21. Rates of nectar production were based on at least 12 inflorescences from each of 15-16 sites in each year. Standard errors to the mean values ranged from 88 to 109. Pollen production was based on measurements of pollen produced by 5 flowers from each of 10 inflorescences from 15-19 sites (1 additional site to the 18 used in 1990). Standard errors of these annual estimates to pollen production ranged from 536 to 1,587.

Floral attribute	1990	1991	1992	1993	1994	1995
inflorescences/ha	6,623	1,117	4,321	8,809	3,821	597
inflorescence length (cm)	[7.59]*	5.12	5.57	6.30	5.08	4.02
nectar production (mg sugar/cm of inflor.)	1,212	719	1,366	2,003	-	-
pollen production (pollen grains/flower)	17,981	7,966	18,752	22,432	-	-

* Inflorescence length measured differently in 1990 and the 1990 measurement gives an inflorescence length approximately 1.5 cm longer than the method used from 1991 onwards.

Table 2.
Availability of nectar at inflorescences of *Banksia ornata* in Ngarkat Conservation Park between 1990 and 1995 in the presence and absence of honeybees.

For each site and distance from an apiary the average quantity of nectar (in grams) was determined for 12-24 inflorescences taken in the late afternoon. The table shows the mean ± s.e for site averages with number of sites given in parentheses. Statistical analyses of these data revealed that the quantity of nectar found in inflorescences close to an apiary (< 300m) was significantly lower than the quantities found at sites not stocked with honeybees in June and early July 1992 and in May, June and July 1993 (ANOVAs and Tukey's tests, p = 0.017, 0.011, <0.001, 0.043 and 0.001 respectively). The quantities found at sites stocked with honeybees but far from the apiary (ie. 900-1000m) were not significantly different from samples taken close to the apiary or from sites without honeybees in 1992 but in 1993 samples from that distance differed from those taken close to an apiary and also from samples taken from sites with no honeybees (Tukey's tests). Nectar levels were lowest close to the apiary and highest at sites not stocked with honeybees. Differences in nectar levels shown in June, July and August 1990 between sites with and without honeybees were not significant (ANOVAs, p = 0.204, 0.356 and 0.237 respectively).

Time of year	Sites stocked with honeybees			Sites not stocked with honeybees
	close to apiary	far from apiary	when honeybees were absent	
1990				
May				2.45 ± 0.40 (9)
June	1.14 ± 0.04 (3)	1.40 ± 0.26 (3)		1.56 ± 0.12 (6)
July	0.59 ± 0.20 (3)	1.22 ± 0.32 (3)		1.00 ± 0.19 (9)
August	0.37 ± 0.16 (4)	0.75 ± 0.12 (4)		0.57 ± 0.11 (8)
1991				
June				0.22 ± 0.08 (15)
July				0.07 ± 0.02 (15)
August				0.002 ± 0.001 (15)
1992				
May			0.83 (1)	2.01 ± 0.08 (2)
June	0.72 ± 0.12 (5)	1.28 ± 0.18 (5)		1.37 ± 0.13 (10)
early July	0.49 ± 0.13 (5)	1.15 ± 0.21 (5)		1.36 ± 0.16 (10)
late July	0.76 ± 0.34 (3)	0.83 ± 0.21 (5)	0.58 (1)	1.03 ± 0.11 (9)
August			0.07 ± 0.06 (3)	0.44 ± 0.18 (6)
1993				
May			2.16 ± 0.09 (6)	1.98 ± 0.10 (6)
May	1.19 ± 0.31 (3)			2.07 ± 0.07 (12)
June	1.65 ± 0.19 (9)	2.07 ± 0.20 (9)		2.43 ± 0.19 (6)
July	1.40 ± 0.17 (9)	2.25 ± 0.14 (9)		2.40 ± 0.22 (6)
August			1.29 ± 0.30 (9)	1.60 ± 0.26 (6)
1994				
July				1.19 ± 0.14 (15)
1995				
late July				0.13 ± 0.05 (17)

Table 3.
Availability of pollen at inflorescences of *Banksia ornata* in Ngarkat Conservation Park from 1990 to 1995 in the presence and absence of honeybees.

The table shows the average numbers of fully laden pollen presenters counted on samples of inflorescences at different distances from apiaries and at sites that were not stocked with honeybees. There were significant differences in the quantities of pollen counted at inflorescences close to apiaries than further away in July 1990, June, July and August 1992, and May, June and July 1993 (ANOVAs, p's <0.001 except for July 1990 when $p = 0.014$ and late July 1992 when $p = 0.006$). In general inflorescences within 350m and 350-700m of an apiary had significantly smaller numbers of fully laden pollen presenters than inflorescences further away. Data show the mean ± s.e. for site and distance averages. At each site and distance the numbers of fully laden pollen presenters were counted for up to 120-300 inflorescences.

Time	Sites without honeybees	Sites stocked with honeybees				
			distance from apiary			
		honeybees absent	<350m	350-700m	800-1200m	1200-1500m
1990						
May	71.7 ± 3.0 (11)					
June	65.4 ± 5.5 (10)		40.1 ± 3.3 (3)		51.6 ± 5.4 (3)	
July	59.8 ± 5.0 (11)		16.2 ± 8.1 (4)	20.2 ± 17.1 (2)	37.8 ± 20.0 (4)	
August	47.4 ± 8.2 (8)		16.6 ± 4.6 (4)	39.7 ± 12.7 (4)	59.9 ± 18.1 (4)	46.9 ±37.0 (4)
1991						
June	10.1 ± 2.4 (15)					
July	15.9 ± 2.2 (15)					
August	9.4 ± 1.5 (15)					
1992						
May	49.4 ± 14.7 (2)		9.2 (1)			
June	64.1 ± 4.3 (10)		8.7 ± 1.8 (5)	18.8 ± 4.0 (5)	44.9 ± 10.1 (5)	53.0 ± 18.2 (3)
early July	52.9 ± 5.9 (10)		5.0 ± 1.9 (5)	6.3 ± 2.6 (5)	11.3 ± 5.3 (5)	21.4 ± 8.5 (5)
late July	46.4 ± 6.0 (8)	27.0 (1)	7.7 ± 0.2 (3)	12.1 ± 3.2 (3)	21.0 ± 9.1 (3)	21.9 ± 9.3 (3)
August	22.1 ± 5.5 (6)	11.7 ± 2.8 (2)	33.2 (1)	30.5 (1)	42.8 (1)	32.3 (1)
1993						
May	69.1 ± 5.6 (6)	69.6 ± 10.4 (5)	8.6 ± 1.8 (4)			
June	56.8 ± 5.9 (6)		10.1 ± 0.6 (9)	15.1 ± 1.4 (9)	31.5 ± 4.2 (9)	35.7 ± 4.8 (9)
July	72.9 ± 6.7 (6)		9.4 ± 1.9 (9)	13.1 ± 3.2 (9)	27.4 ± 4.8 (9)	41.5 ± 7.4 (9)
August	33.2 ± 6.7 (6)	25.5 ± 4.5 (9)				
1994						
July	21.4 ± 4.3 (15)					
1995						
late July	34.2 ± 4.6 (17)					

Table 4.
Quantities of nectar brought back to hives by individual honeybees in 1993. The table shows the volume, concentration and quantity of sugar collected from honeybees in capillary tubes by gently squeezing their abdomens.

20-40 honeybees that were returning to hives (excluding those that returned with pollen) and 20 honeybees that were departing were sampled from different apiaries and on different dates during 1993. The differences between the loads of these two groups of bees were assumed to estimate the net quantities being harvested. The data are means ± s.d.

		Loads carried by bees returning to hives			Loads carried by bees departing hive			Net harvest
Date	Apiary	volume (µl)	concentration (%wt/wt)	sugar (mg)	volume (µl)	concentration (%wt/wt)	sugar (mg)	sugar (mg)
2 June	AL	29.5 ± 5.6 (31)	47.5 ± 7.3 (31)	17.1 ± 4.2 (31)	6.1 ± 2.1 (20)	12.7 ± 2.7 (20)	0.8 ± 0.3 (20)	16.3
3 June	BE	29.7 ± 7.6 (27)	45.6 ± 11.0 (27)	16.8 ± 6.5 (27)	8.2 ± 4.5 (20)	9.7 ± 5.4 (20)	0.7 ± 0.5 (20)	16.1
4 June	MM	30.8 ± 8.0 (31)	45.0 ± 11.0 (31)	17.0 ±6.4 (31)	6.6 ± 3.4 (20)	10.7 ± 4.4 (20)	0.8 ± 0.6 (20)	16.2
14 June	YY	31.3 ± 9.5 (34)	22.5 ± 4.5 (34)	8.0 ± 3.3 (34)	8.4 ± 4.2 (20)	10.0 ± 4.2 (20)	0.8 ± 0.4 (20)	7.2
15 June	WW	26.8 ± 6.4 (20)	27.2 ± 6.1 (20)	8.4 ± 3.0 (20)	7.8 ± 3.4 (20)	10.9 ± 4.6 (20)	0.8 V 0.5 (20)	7.6
5 July	BB	27.9 ± 7.3 (35)	43.2 ± 9.2 (35)	15.0 ± 6.0 (35)	7.8 ± 4.3 (20)	13.4 ± 2.4 (20)	1.1 ± 0.6 (20)	13.9
29 July	OO	27.7 ± 10.9 (25)	46.7 ± 12.1 (25)	17.0 ± 9.6 (25)	5.7 ± 2.5 (20)	15.4 ± 4.5 (20)	1.0 ± 0.6 (20)	16.0
4 August	AA	36.3 ± 6.9 (40)	53.5 ± 6.8 (40)	24.0 ± 6.0 (40)	8.5 ± 2.9 (20)	13.4 ± 4.8 (20)	1.2 ± 0.5 (20)	22.8
Combined		30.4 ± 8.3 (243)	42.1 ± 13.3 (243)	15.6 ± 7.7 (243)	7.4 ± 3.6 (160)	12.0 ± 4.6 (160)	0.9 ± 0.5 (160)	14.5 ± 5.0 (8)

Table 5.
Quantities of nectar and pollen carried by pollen-harvesting honeybees back to hives in 1993.

Values are means ± s.d. with sample sizes in parentheses.

Visual estimate of pollen load		*Banksia ornata* pollen grains	Sugar content of body flw'd (ing)
v		924,908 ± 201,404 *(5)*	5.64 ± 3.*54 (5)*
	L-V	736,932 ± 160,007 *(32)*	4.21 ± 6.*55 (33)*
	L	581,814 ± 152,643 *(23)*	4.10 ± 5.*72 (24)*
	M-L	432,391 ± 129,050 *(17)*	7.91 ± 8.*97 (19)*
	m	381,953 ± 357,180 *(6)*	8.46 ± 8.*37 (9)*
S-M		195,897 ± 32,263 *(10)*	6.40 ± 5.*79 (16)*
S		141,375 ± 60,843 *(6)*	7.93 ± 8.*19 (18)*
	T-S	60,040 ± 18,672 *(6)*	13.10 ± 11.*34 (8)*
	T	48,556 ± 22,056 *(11)*	16.63 ± 7.*99 (18)*
	N-T	24,511 ± 7,082 *(4)*	10.23 ± 10.*77 (5)*

* V = very large; L = large; M = medium; S = small; T = trace; N= negligible: L-V large to very large etc.

Table 6.
Numbers of honeybees returning to hives per day in 1993.

Data are based on measuring rates of return at hourly intervals at 10 hives at each apiary and recording the numbers of honeybees returning with or without pollen. Data are expressed as number of honeybee returns per day per hive. The total amounts of nectar and Banksia pollen collected per hive have been calculated using data in Tables 4 and 5 (i.e. by multiplying the number of returns by the net quantities of nectar or *Banksia* pollen for different sized loads by the average number of returns. For pollen the following values were used 762,000 for very large loads (ie average for V and L-V loads in Table 5), 518,000 for large loads, 266,000 for medium loads, 10 1,000 for small loads and 42,000 for trace loads. For the net quantities of nectar returned by pollen collecting bees the following values were used 3.5 nig, 4.2 ing, 6.6 ing, 7.4 mg and 12.7 ing for very large, large, medium, small and trace loads respectively (these values were calculated from Table 5, based on measurements for the category plus the two adjacent sub-categonies (eg V-L) less the average amount carried on departure (0.90 ing, Table 4).

Site/Apiary:	AL	BE	MM	YY	WW	BB	00			
Date: 2 June	3 June	4 June	14 June		15 June		5 July	29 July		
Returns/day										
nectar	10,944	10,408	33,368	18,949	8,055	19,926	54,780			
pollen	2,202	2,743	2,722	2,445	2,560	3,877	3,778			
total	13,146	13,151	36,090	21,394	10,615	23,803	58,558			
Banksia pollen										
- very large loads			295	483	961	224	25	596	890	
- large loads		848	1018	818	738	309	1520	691		
- medium loads			501	584	413	582	639	1013	702	
- small loads		203	239	224	372	794	440	185		
- trace loads		44	41	157	119	265	175	215		
Other pollens										
- very large loads			15	0	0	0	8	0	68	
-1argeloads		81	28	27	6	54	0	255		
- medium loads			100	174	22	101	116	13	276	
- small loads		115	130	69	210	240	62	325		
- trace loads		0	46	31	92	ill	57	172		
% *Banksia* pollen		85.9	86.2	94.5	83.2	79.4	96.6	71.0		
Sugar (grams)	190.2	181.9	555.9	152.2	79.6	297.9	897.8			
***Banksia* pollen (xlfl~)**			819.7	1,076.6		1,295.1		750.4	440.4	1,562.8
1,250.6										

Table 7.
Net performance of hives of honeybees at Ngarkat Conservation Park 'm 1993.

The table shows the net increase in the quantity of brood, honey and pollen for 10 hives from each of 4 apiaries (40 hives in all) between 1 June 1993 and 27 July 1993. 200 units is equivalent to a full frame.

Attribute of hive	Mean ± s. e (n)
BROOD	
Capped worker	283 ± 26 (40)
Uncapped worker	25 ± 17 (40)
Capped drone	12 ± 3 (40)
Uncapped drone	1 ± 1 (40)
HONEY	
Capped	1,135 ± 93 (40)
Uncapped	234 ± 54 (40)
POLLEN	53 ± 12 (40)

Table 8.
Abundance of honeyeaters at sites stocked and not stocked with honeybees at Ngarkat Conservation Park from 1990 to 1995.

The table shows the mean number of honeyeaters counted per hectare along two 1. 5 lan x 1 00m wide transects (each counted twice) in different months of the year for sites stocked and not stocked with honeybees. The table shows the mean number (± se) of honeyeaters per hectare on a per site basis (ie. n = nwnber of sites counted in each month). For sites stocked with honeybees the mean numbers of honeyeaters counted m three 500m long sections (0-500m, 500- 1 000m, 1000- 1 500m) from an apiary are also given. If reductions of floral resources (nectar, Table 2) affected the numbers of honeyeaters using the mallee-heath habitats then that affect would be expected to be greatest close to an apiary. Analyses of variance revealed that there were no significant reductions in the numbers of honeyeaters recorded close to an apiary cf finther away or between sites stocked and not stocked with honeybees (ANOVAs, p's ranged from 0.43 to 0.78).

Time Sites without honeybees
Sites stocked with honeybees
0-1500M 0-500m 500-1000M 1000-1500m
1990
June
July
August
1991
June
July
1992
June early July late July August August August
1993
June
July
August
1994
2.80 ± 0.52 (4)2.54 ± 0.62 (2)1.98 ± 0.27 (2)2.55 ± 0.60 (2)3.10 ± 1.00 (2)
2.48 ± 0.24 (9)2.69 ± 0.78 (3)3.47 ± 1.43 (3)2.50 ± 0.28 (3)2.10 ± 0.63 (3)
2.92 ± 0.45 (10) 2.64 ± 0.38 (5)2.95 ± 0.48 (5)2.82 ± 0.26 (5)2.14 ± 0.39 (5)
2.09 ± 0.15 (15)
2.20 ± 0.19 (15)
2.10 ± 0.45 (5)2.31 ± 0.65 (5)1.71 ± 0.29 (5)2.29 ± 0.40 (5)
2.49 ± 0.45 (5)2.63 ± 0.41 (5)2.40 ± 0.50 (5)2.45 ± 0.43 (5)
2.95 ± 0.92 (4)3.05 ± 1.39 (4)2.33 ± 0.80 (4)3.18 ± 0.58 (4)
2.93 ± 0.53 (10)
2.16 ± 0.21 (10)
1.92 ± 0.34 (8)
2.16 ± 0.18 (6)
bees present 1.37 (1) 1.10 (1) 1.40 (1) 1.60 (1)
bees removed 1.72 ± 0.44 (2) 1.58 ± 0.73 (2)1.53 ± 0.48 (2)2.05 ± 0.10 (2)

	2.62 ± 0.33 (6)2.17 ± 0.31 (9)2.09 ± 0.24 (9)**2.02 ± 0.37 (9)2.41 ± 0.33** (9)
	3.03 ± 0.33 (6)2.88 ± 0.33 (9)2.81 ± 0.34 (9)2.70 ± 0.23 (9)3.14 ± 0.43 (9)
	2.44 ± **0.45** (6)
	bees removed 2.99 ± 0.32 (9)2.94 ± 0.33 (9)2.68 ± 0.25 (9)3.36 ± 0.38 (9)
July **1995**	3.75 ± 0.25 (15)
	late July 1.40 ± 0.12 (15)

Table 9.
Numbers of Silky Nfice *Pseudo"s apodemoides* and pygmy possums *(Cercartetus spp.)* caught at sites stocked and not stocked with honeybees at Ngarkat Conservation Park.

The table shows means ± s.e. for the number of individuals caught per site during three consecutive ruights, Of trapping using at a single 100m long pitfall line with 10 pits at each site.

Date	Silky Mce	Possums		
	sites without honeybees	sites with honeybees	sites without honeybees	sites with honeybees
June 1990	8.08 ± 0.92 (13)	11.60 ± 1.81 (5)	1.08 ± 0.42 (13)	1.40 ± 0.51 (5)
Aug. 1990	15.08 ± 1.91 (13)	18.20 ± 2.73 (5)	0.38 ± 0.27 (13)	1.40 ± 0.93 (5)
Jul-Aug. 1991	3.60 ± 0.71 (15)	0.13 ± 0.09 (15)		
Aug. 1992	5.50 ± 1.11 (10)	6.80 ± 2.29 (5)0.50 ±0.40 (10)	0.40 ± 0.24 (5)	
Aug. 1993	15.2 ± 15.7 (6)4.78 ± 1.12 (9)0.67 ± 0.49 (6)1.33 ± 0.50 (9)			
Aug. 1994	2.13 ± 0.38 (16)	0.19 ± 0.14 (16)		
Aug, 1995	2.42 ± 0.51 (12)	0.0 ± 0.0 (12)		

Table 10.
Intensity of use of *Banksia ornata* inflorescences by small mammals at sites stocked and not stocked by honeybees and with distance from an apiary at Ngarkat Conservation Park.

The table gives the percentage of inflorescences that carried mammal scats at different sites and distances from an apiary in different months and years. Estimates of the proportion of inflorescences carrying mammal scats were based on observations made at least 60 and up to 240 inflorescences for the different distances from an apiary, and up to 540 inflorescences at sites not stocked with honeybees. Samples sizes were smaller in 1991 and 1995 when poor floral abundances reduced sample sizes to around 30 inflorescences. Values are means ± s.e for replicate counts made at different sites. Statistical analyses of these data revealed that there were no significant differences in the per cent of inflorescences carrying faem with distance from an apiary or at sites without honeybees in June, July and August 1990, in June, early July and late July 1992, nor in June and July 1993 (ANOVAs, p's = 0.31, 0.66, 0.99, 0.08, 0.52, 0.97, 0.64 and 0.39 respectively). However, there were significantly more inflorescences with faeces at sites stocked with honeybees in May 1993 compared with sites not stocked with honeybees in that month (t-test,
p = 0.005).

Time	Sites not stocked with											
honeybees		0- 350m		350-700m		800-1200m		1200-1500m				
Sites stocked with honeybees												
1990												
	May	1.1 ± 0.3 (11)										
	June	1.0 ± 0.2 (11)		0.6 ± 0.4 (3)		0.6 ± 0.6 (3)		0.0	0.0 (3)	1.7 ± 1.0 (3)		
	July	2.1 ± 0.7 (11)		0.7 ± 0.4 (4)		0.9 ± 0.8 (3)		2.8	2.3 (4) 0		(1)	
	August	14.9 ± 6.0 (9)		17.1 ± 12.4 (4)		14.5 ± 10.3 (4)		15.5	13.5 (4)	14.4 ± 14.4 (2)		
1991												
	June	15.6 ± 5.5 (15)										
	July	12.1 ± 4.5 (15)										
1992												
	May	0.6	0.6 (2)	2.8	(1)							
	June	1.2	0.4 (10)	3.6 ± 2.0 (5)		3.0 ± 1.4 (5)		0.2 ± 0.2 (5)		16.7	15.0 (3)	
	car. July		0.9	0.4 (10)	4.5 ± 2.6 (5)		3.0 ± 2.1 (5)		2.6 ± 2.2 (5)		2.0	1.0
(5)												
	late July		5.5	2.2 (9)	6.9 ± 2.5 (3)		5.9 ± 3.6 (3)		5.6 ± 3.1 (3)		3.6	2.5
(3)												
August	18.9 3.9 (8)		3.5	(1)	6.1	(1)	2.8	(1)	4.4	(1)		
1993												
	May	1.1	0.6 (11)	10.8	5.5 (4)							
	June	2.3	0.7 (6)	5.0	1.7 (9)	6.6 ± 3.1 (9)		3.1 ± 1.3 (9)		4.8	1.8 (9)	
	July	1.2	0.5 (6)	8.4	2.7 (9)	5.7 ± 2.8 (9)		3.9 ± 2.0 (9)		5.3	1.9 (9)	
	August	18.2	3.3 (15)									
1994												
July	2.3 ± 0.2 (15)											
1995												
late July	17.6 ± 3.6 (17)											

Table 11.
Distribution and abundance of honeybees using *Banksia ornata* inflorescences 'm Ngarkat Conservation Park at sites stocked and not stocked with honeybees between 1990 and 1995.

Data are expressed as the numbers of honeybees per 1000 inflorescences and are based on counts of insects at samples of 60-540 *Banksia omata* inflorescences taken between 1030 and 1400h in 1990, 1992 and 1993. Sample sizes were smaller in 1991, 1994 and 1995 in part because there were fewer inflorescences available to be scored in those years. Samples sizes in those years were usually around 30 inflorescences. The table shows means ± s.e for replicate sites. There were significantly higher numbers of honeybees working inflorescences of *Banksia ornata* at sites with apiaries particularly close (<350m) to an apiary in July 1990, August 1990, June 1992, early and late July 1992, June 1993 and July 1993 (ANOVAs and Tukey's tests, p's <0.001 exceptmi June 1990 when p = 0.017 and late July 1992 when p = 0.034).

Time	Sites not stocked with honeybees	Sites stocked with honeybees 0- 350m	350-700m	800-1200m	1200-1500m
1990					
May	0.3 ± 0.3 (11)				
June	3.4 ± 2.6 (11)	83.2 ± 28.7 (3)	11.1 11.1 (3)	32.8 ± 32.8 (3)	27.8 ± 27.8 (3)
July	2.1 ± 1.0 (11)	132.2 ± 64.9 (4)	127.8 68.3 (3)	28.3 ± 21.5 (4)	0 (1)
August	1.0 ± 1.0 (9)	142.3 ± 30.0 (4)	33.5 12.0 (4)	21.2 ± 13.0 (4)	0.0 ± 0.0 (2)
1991					
June	22.2 ± 22.2 (15)				
July	3.3 ± 2.4 (15)				
1992					
June	4.7 ± 4.7 (10)	299,5 ± 86.7 (5)	66.0 ± 33.5 (5)	38.9 ± 36.2 (5)	0.0 0.0 (3)
ear. July	14.2 ± 8.2 (10)	479.9 ± 92.6 (5)	225.0 72.6 (5)	118.9 53.9 (5)	123.3 45.8 (5)
late July	3.2 ± 2.0 (9)	116.3 ± 59.7 (3)	30.6 14.7 (3)	22.2 14.7 (3)	77.8 53.0 (3)
August	15.8 ± 5.5 (8)	0 (1)	0 (1)	0 (1)	14.7 (1)
June	9.0 ± 6.1 (6)	231.6 ± 38.0 (9)	77.8 20.9 (9)	52.2 ± 20.1 (9)	15.4 ± 6.6 (9)
July	17.8 ± 13.7 (6)	293.5 ± 57.0 (9)	136.7 31.1 (9)	40.7 ± 18.9 (9)	27.8 ± 8.8 (9)
August	5.4 ± 2.5 (15)				
1994					
July	15.7 ± 9.5 (15)				
1995					
late July	1c) +_ 3 ~ (0 7)				

Table 12.
Distribution and abundance of native bees using *Banksia ornata* inflorescences 'm Ngarkat Conservation Park at sites stocked and not stocked with honeybees between 1990 and 1995.

Data are expressed as the numbers of native bees per 1000 inflorescences and are based on counts of insects at samples of 60-540 *Banksia ornata* inflorescences taken between 1030 and 1400h in 1990, 1992 and 1993. Sample sizes were smaller in 1991, 1994 and 1995 in part because there were fewer inflorescences available to be scored in those years. Samples sizes in those years were usually around 30 inflorescences. The table shows means ± s.e for replicate sites. Ihere were no significant differences in the numbers of native bees working inflorescences of *Bardaia omata* at sits with and without honeybees and with distance from an apiary in June 1990, July 1990, June 1992, early and late July 1992, June 1993 and July 1993 (ANOVAs, p's = 0.80, 0.24, 0.52, 0. 12, 0.14, 0.25, and 0. 16 respectively).

Time	Sites not stocked with										
honeybees		0- 350m		350-700m		800-1200m		1200-1500m			
Sites stocked with honeybees											
1990											
	May										
	June										
	July										
August											
0.3 ± 0.3 (11)											
1.0 ± 0.8 (11)											
1.4 ± 0.5 (11)											
0.0 ± 0.0 (9)											
1991											
June	*107.6 ± 14.0 (15)*										
July	*15.9 ± 3.6 (15)*										
1.1	1.1 (3)	0.0	0.0 (3)	1.9 ± 1.9 (3)		0.0 ± 0.0 (3)					
2.4	1.4 (4)	0.0	0.0 (3)	4.8 ± 2.9 (4) 0		(1)					
1.2	1.2 (4)	0.0	0.0 (4)	4.2 ± 4.2 (4)		0.0 ± 0.0 (2)					
1992											
	May	*5.6 ± 5.6 (2)*		*0.0*	*(1)*						
	June	*2.0 ± 1.7 (10)*		*11.7 ± 7.2 (5)*		*5.5 ± 3.8 (5)*		*13.3 13.3 (5)*		*0.0 ± 0.0 (3)*	
	ear. July		*3.1 ± 1.1 (10)*		*15.1 ± 5.5 (5)*		*20.0 ± 9.4 (5)*		*14.4 6.5 (5)*		*30.0 ± 15.3*
(5)											
late July		*6.2 2.1 (9)*		*16.6 ± 7.0 (3)*		*13.9 ± 2.8 (3)*		*16.7*	*9.6 (3)*	*38.8 ± 24.2 (3)*	
August	*13.4 6.2 (8)*		*0*	*(1)*	*0*	*(1)*	*0*	*(1)*	*0*	*(1)*	
1993											
	June	*12.0*	*6.0 (6)*	*3.7 ± 2.6 (9)*		*9.3 ± 2.1 (9)*		*5.6 ± 2.8 (9)*		*3.3*	*2.2 (9)*
	July	*2.8*	*1.8 (6)*	*0.9 ± 0.9 (9)*		*1.5 ± 1.0 (9)*		*7.4 ± 2.9 (9)*		*5.6*	*2.8 (9)*
August	*1.9 ± 0.8 (15)*										
1994											
July	*11.8 ± 6.4 (15)*										
1995											
late *July 2.0 ± 2.0 (17)*											

Table 13.
Distribution and abundance of ants using *Banksia ornata* inflorescences 'm Ngarkat Conservation Park at sites stocked and not stocked with honeybees between 1990 and 1995.

Data are expressed as the numbers of ants per 1000 inflorescences and are based m counts of insects at samples of 60-540 *Banlaia ornata* inflorescences taken between 1030 and 1400h in 1990, 1992 and 1993. Sample sizes were smaller in 1991, 1994 and 1995 in part because there were fewer inflorescences available to be scored in those years. Samples sizes in those years were usually around 30 inflorescences. The table shows means ± s.e for replicate sites. There were no significant differences in the numbers of ants working inflorescences of *Banksia ornata* at sites with and without honeybees and with distance from an apiary in June 1990, July 1990, August 1990, June 1992, early and late July 1992, June 1993 and July 1993 (ANOVAS, p's = 0.95, 0.14, 0.29, 0.94, 0.21, 0.69, 0.67, and 0.89 respectively).

Time	Sites not										
	stocked with										
honeybees		0- 350m		350-700m		800-1200m		1200-1500m			
Sites stocked with honeybees											
1990											
	May										
	June										
	July										
August											
	74.6	18.6 (11)									
	29.5	14.9 (11)									
	30.3	6.9 (11)									
	18.5	5.8 (9)									
1991											
	June	519.5 ± 204.9 (15)									
July	305.9 ± 95.8 (15)										
45.0 ± 25.9 (3)		33.3 ± 33.3 (3)		25.7	15.8 (3)	61.1 ± 33.8 (3)					
7.8 ± 4.8 (4)		37.0 ± 37.0 (3)		25.0	12.3 (4)		0	(1)			
10.8 ± 4.4 (4)		6.3 ± 6.3 (4)		4.2	2.4 (4)	12.5 ± 12.5 (2)					
1992											
	100.0 ± 33.3 (2)		166.7	(1)							
	June	47.2 ± 10.7 (10)		43.9 ± 15.3 (5)		42.5 ± 7.1 (5)		44.4	20.3 (5)	66.7 ± 50.9 (3)	
ear. July		41.1 ± 6.9 (10)		72.6 ± 20.3 (5)		111.7 ± 45.1 (5)		130.0	5.9 (5)	73.3 ± 19.4 (5)	
late July		69.1 ± 19.3 (9)		34.2 ± 11.4 (3)		41.7 ± 21.0 (3)		50.0	9.6 (3)	72.2 ± 5.6 (3)	
August	50.3 ± 14.6 (8)		6.9	(1)	0	(1)	0	(1)	14.7	(1)	
1993											
	June	77.9	21.6 (6)	60.7	18.8 (9)	96.0	25.7 (9)	63.1 ± 19.6 (9)		100.4	31.9 (9)
	July	48.9	16.0 (6)	29.6	9.5 (9)	30.6	7.3 (9)	39.9 ± 15.5 (9)		37.0	15.4 (9)
	August	96.5	22.0 (15)								
1994											
July											
439.1± 90.4 (15)											
1995											
late July	621.1 ± 87.5 (17)										

Table 14.
Patterns of seed production by *Banksia ornata* in Ngarkat Conservation Park at sites stocked and not stocked with honeybees.

At each site and sampling time, 10-50 inflorescences were tagged near the centre of each site and left alone to measure natural rates of seed production. A second sample of 10-50 inflorescences were also tagged in the same area and given additional pollen once every 3 days while flowering, except in 1990 when each inflorescence was only given additional cross pollen on one occasion. Seed production at these inflorescences was then scored approximately nine months later and the mean number of seeds produced per inflorescence calculated for each treatment at each site. The data in this table show the means of those means s.e) for replicate sites that had and did not have honeybees. The number of replicates were reduced in 1990 because most of the sites were burnt in December 1990 before the number of seeds in infructescences had been scored. Four sites, three not stocked with honeybees and one that had been, were not burnt. A second site stocked with honeybees in 1990 was only partially burnt and most inflorescences were not burnt at this site. 10 inflorescences were used per sample in June 1990, 30 in July 1990, 20 in July 1991, 50 in June 1992 and 25-50 inflorescences in July and August 1993. Natural rates of seed production were higher at sites stocked with honeybees thari those without honeybees in June 1990, July 1990, July 1992 and early July 1993 (t-tests, p's < 0.00 1 except 'm June 1990 when p = 0.07). 'Me addition of pollen to inflorescences increased seed production at sites not stocked with honeybees in June 1990, July 1990, July 1992, early July 1993 and late August 1993 (t-tests, p's = 0.06, 0.02, <<0.00 1, <<0.00 1, and 0.002 respectively) but not in July 1991 (p = 0.324). Addition of pollen to inflorescences exposed to honeybees did not result in significantly higher seed production (p's > 0. 1) except in early July 1993 (t-test, p = 0.0 12)

Time	Sites not stocked with honeybees		Sites stocked with honeybees	
	natural	additional	natural	additional
1990				
June	3.49 ± 0.*80 (3)*	6.03 ± 1.*00 (3)*	9.33 *3.58 (2)*	9.50 *2.30 (2)*
July	3.07 ± 0.91 (3)	6.20 ± 0.*54 (3)*	12.51 *0.19 (2)*	10.54*1.74 (2)*
1991				
July	4.64 ± 0.*71 (15)*	3.85 ± 0.*35 (15)*		
1992				
july	5.49 ± 0.*54 (10)*	9.24 ± 0,59 *(10)*	8.32 ± 1.*03 (5)*	9.84 ± 0.*86 (5)*
1993				
early July	7.32 ± 0.*64 (6)*	11.47 ± 0.*24 (6)*	10.92 ± 0.*54 (9)*	12.20 ± 0.*62 (9)*
late August	7.25 ± 0.*41 (15)*	8.92 ± 0.*33 (15)*		

Table 15.
Pattern of seed production for *Banksia omata* with distance from an apiary.

Seed production was measured at 1 00m, 500m, 1 000m and 1500m at six to eight sites stocked with honeybees in July 1993. The table shows means of site averages for each distance and data for 13 locations without honeybees where seed production was measured at the same time. At each site a second sample of inflorescences were given additional pollen and data for this treatment is given as well.

Distance from apiary
Seeds/inflorescence
natural additional

6.08 ± 0.59 (13)
No honeybees
loom
500m
1000m
1500m
10.73 ± 0.57 8)
10.57 ± 0.64 7)
8.33 ± 1.08 (6)
7.57 ± 0.90 (6)
10.84 ± 0.50 (13)
12.09 ± 0.64 8) 11.70 ± 0.78 7) 10.09 ± 0.71 6)
10.64 ± 0.936)
