OVERVIEW OF THE IMPACTS OF FERAL AND MANAGED HONEYBEES IN AUSTRALIA

invasive species program

Australian Nature Conservation Agency

OVERVIEW OF FERAL AND MANAGED HONEYBEES IN AUSTRALIA:

DISTRIBUTION, ABUNDANCE, EXTENT OF INTERACTIONS WITH NATIVE BIOTA, EVIDENCE OF IMPACTS AND FUTURE RESEARCH.

by

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The views and opinions expressed in this report, are those of the authors and do not necessarily reflect those of the Commonwealth Government, the Minister for the Environment or the Director of National Parks and Wildlife.

CONTENTS

FOREWORD

The impact of introduced species on native populations is usually assumed to be negative, but as you will see from this overview, feral honeybees can produce both positive and negative effects on native plants and animals. In this report it is shown that feral honeybees can enhance the seed production of a number of native plants whose native pollinators have declined substantially due to a variety of factors. It has also shown that feral honeybees can reduce the seed production of other native plants and compete with honeyeaters for nectar.

These varying effects on the native environment show that it is important to quantify the impact of feral animals on native species before any management decisions are made. It may be beneficial to leave the system as is if introduced animals are compensating for a decline in native species. However, if the impact is determined to be negative to the natural environment, then strategic control operations and appropriate management strategies are justified.

This series of national overviews was commissioned by the Invasive Species Program to comprehensively assess the information, available on a range of introduced species and serves to highlight key gaps in our knowledge. I trust that this series of overviews will be a useful tool when considering future research to enhance our knowledge base.

Peter Bridgewater
 Chief Executive Officer
Australian Nature Conservation Agency

SUMMARY

Feral and managed colonies of honeybees have been present in Australia for about 170 years, but their distribution and abundance has increased dramatically over the last 60 years. There are over 500,000 managed hives in Australia and an unknown number of feral colonies. Managed colonies are patchily distributed in time and space, with beekeepers usually shifting loads of around 100 hives into and out of areas for 2-4 month periods coinciding with peaks in flowering of key plants (often species of Eucalyptus). A concentration of 100 hives at the site of an apiary is only equivalent to about 0.1 colonies per hectare, because honeybees forage out to distances of at least 2 km from their hives, covering at least 12 km^2. Feral colonies are also patchily distributed being least abundant, if not absent, from alpine areas and inland areas away from water. Limited quantitative data show densities ranging from 0.001 feral colonies per hectare in inland mallee-heaths to locally high densities of 0.77 colonies per hectare in riparian woodlands. Locally high densities, however, may reflect restricted availability of suitable hollows and not effective densities in the area as a whole.

The hollows used by feral honeybees broadly overlap with those used by a variety of native birds and mammals, but feral colonies appear to occupy only a small proportion of the available hollows (often < I%). This suggests that interactions between feral colonies and hollow-nesting Australian fauna may not be substantial but few studies have adequately assessed the availability of suitable hollows, particularly their internal characteristics.

Honeybees visit the flowers of at least 200 Australian plant genera and interact with a wide diversity of native flower-visiting animals. For many plants, honeybees were the most frequent floral visitors, and often consumed more than half of the floral resources' being produced.

Numbers of native bees may decline following influxes of honeybees into an area but data on this relationship were equivocal. Reproductive performances of several species of native bee also did not change dramatically following influxes of honeybees to areas. However, honeybee densities may not have been manipulated adequately to cause a measurable response, and second order interactions involving responses by predators or parasites may have disguised the responses of native bees.

Responses of honeyeaters to influxes of honeybees varied. In Banksia ornata heathlands where there was a surplus of floral resources the numbers of honeyeaters did not change following influxes of honeybees, but at patches of Callistemon rugulosus New Holland Honeyeaters increased the sizes of their feeding territories and reduced the frequency with which flowers were visited. Population densities in patches of Callistemon were reduced by 30-50% when honeybees were prominent.

Honeybees also influenced the production of seeds by various plants. At some plants seed production was reduced when honeybees were frequent floral visitors (eg C. rugulosus) while at others seed production was enhanced (eg B. ornata). Plant species whose seed production increased were those that received inadequate attention from their native pollinators. Plantpollinator systems are vulnerable to perturbations like habitat clearance and degradation, and some Australian plants may now depend on honeybees for full pollination because their native pollinators have declined dramatically or even disappeared in some areas.

Whether honeybees should be included or excluded from selected areas will depend on which native taxa are to be favoured in those areas. Some plants may benefit by the presence of honeybees while other plants and animals may continue to suffer degradation in their presence.

Future research should measure the effects of honeybees on a wide diversity of native flora and flower-visiting fauna to firmly establish the extent of detrimental interactions. Both descriptive and experimental studies are needed. The spatial and temporal scales of manipulative experiments must be carefully considered. Manipulations that reduce rather than increase the numbers of honeybees working flowers in an area may be more relevant to future management programs that are likely to reduce the numbers of honeybees in an area. Some priority should also be given to studies on the population dynamics of feral colonies of honeybees and broadacre methods of efficiently removing feral colonies from selected areas.

Management of honeybees in areas set aside for conservation will remain contentious while there is insufficient information about interactions between honeybees and the Australian biota. A regional approach that leads to at least some of the natural resources within each region being maintained free from honeybees would promote conservation of regional biodiversity and provide an alternative management strategy that is not reliant on measuring the effects of honeybees on natural systems. Ultimately effective management of honeybees and natural resources will depend on cooperation from the beekeeping industry.

Disclaimer

ACKNOWLEDGEMENTS

1. INTRODUCTION

Since the late 1970s there has been growing concern amongst conservationists, ecologists and land managers that the presence of honeybees in conservation areas may conflict with the primary purpose of those reserves - the conservation of Australia's endemic flora and fauna. Honeybees may outcompete native fauna for floral resources, may disrupt natural pollination processes and may displace endemic wildlife from tree hollows. Numerous authors have presented arguments for and against the need to exclude honeybees from conservation areas (Matthews 1984; Bell 1987; Thorp 1987; Hopper 1987; Stace 1988; Manning 1989, 1993a; Anderson 1989; Pyke 1990; Paton 1993). The lack of consensus reflects the biases of individual contributors and the dearth of good quality research on interactions between honeybees and Australian biota. That some of the initial research on impacts has been equivocal has not helped (Pyke and Balzer 1985; Sugden and Pyke 1991). Most reviews, however, have concluded that differences of opinion will only be resolved with further research.

This report summarises and critically reviews research on the impacts of honeybees on Australian flora and fauna, and recommends the future research needed to develop effective management strategies for honeybees in the Australian environment. A key issue in this process is to separate the impacts of feral honeybees on Australian biota from those of commercially-managed honeybees.

The review has four parts. The first part examines information on the distribution, abundance and behaviour of both feral and managed colonies of honeybees in Australia. Subsequent parts summarise and assess evidence on interactions between honeybees and Australian biota, the management of honeybees in Australia, and possibilities for future research.

2. THE DISTRIBUTION AND ABUNDANCE OF HONEYBEES IN AUSTRALIA

Managed hives of honeybees

Honeybees Apis *mellifera* were first introduced to Australia in 1810 by Samuel Marsden who imported an unknown number of colonies from England. These, however, failed to establish and eventually died out as did the hive introduced to Tasmania in 1821 (Ziegler 1993). A second introduction in 1822 to mainland Australia was successful and further introductions to other parts of the continent over the next 50-60 years introduced other races and apiaries were established in each state (Eagland 1958; Manning 1989, 1992; Wills 1989; Oldroyd *et al.* 1993; Ziegler 1993). Despite these introductions honeybees were probably not widespread until about 1930 when beekeepers were able to travel more easily; from then the honeybee industry grew steadily (Manning 1992). For example, the average yearly production of honey in Australia from 1921-25 was 3200 tonnes but by 1949-54 there were some 442,000 commercially managed hives producing about 12,500 tonnes of honey annually (Eagland 1958). By 1971-72 524,000 hives in Australia produced 22,000 tonnes of honey per annum (Read 1972) and in the 1980s approximately 546,000 hives produced 25,400 tonnes of honey annually (Wills 1989). Thus since the 1920s honey production has increased eight-fold despite further and substantial clearance of native vegetation (eg Harris 1976; Cook 1987; Saunders *et al.* 1990).

Wills (1989) compiled statistics on the numbers of beekeepers and managed hives in each of the states in the 1980s (table 1). Of the states, New South Wales (NSW) supported the largest number of beekeepers and the most beehives (over 210,000). Queensland (Qld), Victoria (Vic) and South Australia (SA) each had around 84, 000 hives, Western Australia (WA) 44,000, and Tasmania (Tas) 12,000. Statistics for the Northern Territory (NT) and Australian Capital Territory (ACT) were not provided but these territories have at most a few thousand managed hives.

Table 1 Approximate numbers of hives of honeybees maintained by beekeepers in each Australian state during the 1980s (based on Wills 1989). The table shows the average numbers of hives kept per year in each state over a period of up to five years between 1979 and 1986; numbers of managed hives fluctuated between years by up to 30,000 hives or 25% of the mean in some states. Only beekeepers with at least 40 hives are included. At least another 3000 amateur beekeepers kept fewer than 40 hives each (Read 1972); these are included in no. of hives. The discrepancy between the state and Australian totals is because different five-year periods were used.

State	No. of beekeepers	No. of hives
Queensland	370	83, 110
New South Wales	818	211, 614
Victoria	408	84, 487
Tasmania	59	12, 480
South Australia	344	85, 406
Western Australia	151	43, 640
Australia	2213	546, 200

Precise information on the distribution of managed hives in each of the states is not available. This reflects the difficulty of collating accurate information on the movements of beekeepers; the movements of apiaries vary from year to year with the availability of floral resources. Manning (1992, 1993b), however, provides information on the distribution of 3475 apiary sites in WA (2436 registered apiary sites on crown land; 1039 sites on private land based on responses from 69% of WA's beekeepers) and some information on patterns of seasonal and annual use. The apiary sites were clustered into a number of key regions mostly in an area south of Geraldton and west of Albany. Both commercial and non-commercial beekeepers used these sites and not all sites were used in each year. Sites used by commercial beekeepers were usually stocked with about 100 hives for an average of 12 weeks, while those used by non-commercial beekeepers were stocked on average with about 60 hives for 26 weeks. A few sites were stocked with beehives throughout the year and others for as little as 3-4 weeks at a time.

Elsewhere in Australia, commercial beekeepers typically stock apiary sites at similar densities (ca 100 hives) for similar durations (2-4 months; table 2) and have some sites that are used each year and others that are used less depending on flowering levels. Detailed knowledge of the distribution of managed colonies, however, is not available. Most states hold files that list the locations of registered apiary sites within reserves but do not maintain records on the frequency and extent to which those sites are used by beekeepers.

Table 2 Patterns of use of floral resources by commercial beekeepers in different parts of Australia. The symbols show the months of the year when particular floral resouces are used by beekeepers. Only a selection of resources are shown to illustrate patterns of use. Information- provided by beekeepers, State Apiary Officers and others (eg Wills 1989; Manning 1992). No information provided on patterns of use of floral resources by commercial beekeepers for NSW and Qld. Most regions broadly defined and local movements of apiaries between floral resources may occur. Thus these patterns may over-estimate the length of time an apiary site is occupied.

State and region	J	F	M	A	M	J	J	A	S	O	N	D	Main floral resources
TAS													
N & NW	~	~									~	~	blackberry, clover
E coast									~	~	~		*Eucalytpus globulus*
S		~	~								~	~	prickly box, clover etc
W	~	~	~	~									*Eucryphia* spp
SA													
SE region													
Salt Creek/Ngarkat					~	~	~	~					Banksia *ornata*
Keith-Coonalpyn								~	~	~	~		various eucalypts
Bordertown-Padthaway	~										~	~	*Eucalyptus leucoxylon*
Peebinga-Lameroo	~	~	~	~				~	~	~	~		various mallee eucalypts
Keith-Bordertown	~	~	~										lucerne
Bangham area			~	~									*E. baxteri*
Millicent area	~	~	~								~	~	conola, carrots, clover
Robe area			~	~									*Melaleuca lanceolata*
Riverland													
Loxton-Waikerie		~									~		various eucalypts/ mallees
Loxton-Waikerie								~	~	~			almonds, oranges, apricots
Mt Lofty Ranges/Adelaide Plains													
McLaren Vale								~	~				almonds
Mt Lofty Ranges		~										~	*Eucalyptus camaldulensis*
Fleurieu Peninsula		~	~	~									*E. baxteri, E.,obliqua*
Mt Lofty Ranges			~	~	~								*E. microcarpa*
Mt Lofty Ranges													*E. cosmophylla*
St Vincent Gulf		~	~										Avicennia *officianalis*
Mt Lofty Ranges				~	~	~	~	~	~	~	~	~	*E. leucoxylon*
Mid-North/Flinders R													
S Flinders Ranges								~	~	~	~		*E. leucoxylon, Echium*
S Flinders Ranges		~	~										*Eucalyptus cladocalyx*
S Flinders Ranges		~	~	~									*E. microcarpa*
N Spencer Gulf		~	~	~									*Avicennia officinalis*

State and region	J	F	M	A	M	J	J	A	S	O	N	D	Main floral resources
Mid-North	~	~	~								~		Strawberry clover
Mid-North				~	~	~	~	~	~	~	~	~	*E. leucoxylon*
Mid-North									~	~	~	~	Echium
Mid-North			~	~									*Eucalyptus microcarpa*
Yorke Peninsula		~	~	~	~								*Melaleuca lanceolata*
Yorke Peninsula					~	~	~	~					*E. diversifolia, Acacia*
Yorke Peninsula	~	~									~	~	various mallee eucalypts
Eyre Peninsula													
Elliston area				~	~	~	~	~	~				*E. diversifolia*
lower Eyre Peninsula	~	~	~										*E. cladocalyx*
scattered sites	~	~	~	~	~	~	~	~	~	~	~	~	mallee eucalypts
Kangaroo Island													
forests	~	~	~										*E. cladocalyx*
mallee-heaths/farmland			~	~	~								*E. porosa, E. cosmophylla*
mallee-heath/scrub									~	~	~	~	*E. diversifolia/ fasciculosa*
WA													
Perth-Geraldton (N sandplain)				~	~								various *Banksia*
sandplain)					~	~	~	~	~				various shrubs/trees
Payne's Find area								~	~	~	~		*E. loxophleba*
Eastern Goldfields	~								~	~	~		various eucalypts
Perth-Bunbury (forests)	~	~	~								~	~	*E. marginata, E. calophylla*
Bunbury-Walpole area			~	~									*E. diversicolor*
Ravensthorpe area	~	~	~	~	~	~					~	~	*E. occidentalis/* coast.hths
N State Forests	~										~		*E. marginata, B. grandis*
S Forests		~	~	~	~	~							*E. diversicolor, E. calophylla*
Yanchep/Dongara (coastal pln)				~	~	~	~	~	~	~			Banksia, Leucopogon, *Dryandra, Hakea*
NT													
Top End								~	~	~	~	~	*Melaleuca* sp
Katherine area	~	~	~								~	~	melons, other crops

The presence of 100 hives at an apiary suggests that there will be intense use of floral resources immediately around that apiary. However, although the density of colonies at the site of an apiary is high, bees from these hives forage over an extensive area around the apiary. Overseas figures suggest that most honeybees forage within 2-3 km of their hives but may travel as far as 14 km when resources are poor (Gary *et al.* 1977; Eickwort and Ginsberg 1980; Visscher and Seeley 1982; Seeley 1985; Winston 1987; Roubik 1991). Sugden and Pyke (1991) estimated that honeybees foraged out to distances of about 2 km from hives in Nadgee Nature Reserve, NSW during spring and summer, while Paton *et at. (MS 1;* unpubl.) showed that most bees from commercial apiaries foraged mainly within 1 km of their hives while exploiting floral resources of *Banksia ornata* in Ngarkat Conservation Park (CP) during winter. The bees travelled further distances from their hives in warmer weather and when resources were less abundant. If we assume that most honeybees forage within 2 km of their hives then the hives

present at an apiary are effectively distributed over an area of about 12 km^2 (1200 ha). With a hundred hives this is equivalent to an effective density of 0.1 colonies per hectare (col/ha). In most states the distances between commercial apiary sites on public land (reserves) is around 1.5-2 km. If all sites are occupied at the same time then effective densities for managed hives may approach 0.2-0.3 col/ha but usually not all sites are occupied simultaneously (G Cotton pers. comm.; D Paton pers. obs.). In Queensland registered sites on public land are 0.8 km apart while in WA they are usually at least 3.0 km apart (information from S Bryce, CALM, WA).

Feral colonies of honeybees

Historical information on the distribution and abundance of feral honeybees in Australia is largely lacking. Feral colonies would have established shortly after the introduction of managed hives and slowly spread away from these sites. In Tasmania, feral swarms were first noted in 1838 just 7 years after successful establishment, and before long were reported widely over the island (Ziegler 1993). Similarly, in New Zealand feral colonies of A. *mellifera* were reported occupying many hollow trees within nine years of the initial introduction (Donovan 1980). How quickly they spread across the Australian mainland is difficult to judge. The distances moved by swarms from a parent colony in other countries varies from as little as 50 m to over 4 km, the distances depending on the race of honeybee and presumably on the availability of resources (Winston 1987). Most swarms, however, settle within 1 km of the parent colony. Given sufficient time feral colonies may have preceded the spread of commercial apiaries into some areas. For example, Manning (1992) states that swarms of honeybees were first seen in the Ravensthorpe area of WA in about 1925 but commercial beekeepers did not start operating in that area until 1930.

Feral colonies are now widespread though patchily distributed over the Australian mainland (table 3). Areas believed to have high densities include: mallee regions and riparian habitats along watercourses in north-eastern Victoria particularly redgum/black box habitats; coastal woodland areas of south-western WA; coastal

regions, creeklines and sugar gum woodlands of Kangaroo Island; woodland areas in the south-eastern parts of South Australia (particularly west of Keith); parts of Yorke Peninsula and the west coast of South Australia; and possibly the wetter coastal woodland areas of Queensland. Areas assumed to have low densities include alpine areas and and inland areas away from water courses. Factors that may limit the distribution of feral colonies in these regions include: availability of water; availability of food; availability of suitable hollows; various bee diseases; and cold or wet weather.

Quantitative data on the numbers of feral colonies in different parts of Australia are largely lacking. Manning (1992) collated qualitative information on the numbers of feral colonies in regions of WA. Each region was defined by a 1:50,000 Topographic Series map (equivalent to about 600 km^2). Feral colonies were present in virtually all regions throughout the south-western third of WA. However, the relative densities estimated by beekeepers on a crude scale of low, medium and high often varied within a region and these densities were not defined.

Paton *et at.* (MS2) have counted and monitored feral colonies in an area of about 200 ha around the SA National Parks and Wildlife Service (NPWS) Headquarters at Rocky River within Flinders Chase National Park (NP) on Kangaroo Island. The area searched consisted of extensive areas of tall sugar gum, *Eucalyptus cladocalyx* forest and woodland interspersed with stands of *E. divers folia, E. ovata* and *E. fasciculosa* and areas of mallee heath and modified grasslands with scattered trees. In this area densities fluctuated from 0.2 to 0.4 col/ha over a three year period but were usually maintained near 0.3 col/ha. Within localised areas the highest densities exceeded 10 col/ha. In other parts of South Australia, densities ranged from 0.001-0.004 col/ha (in mallee heath) to 0.1-0.4 col/ha in remnant eucalypt woodland in the Mt Lofty Ranges (table 4; Paton *et al.* MS2, unpubl.).

The only other data available are for the river redgum, E. *camaldutensis* and black box, *E. largiflorens* habitats of Wyperfeld National Park where densities have been measured at 0.77 col/ha (Oldroyd et *al. 1994).* These densities, however, overestimate the densities within the reserve, since the survey was restricted to riparian woodlands known to

house feral colonies. Riparian woodlands represent only a small proportion of the reserve, and the other more extensive habitats within the reserve are likely to be relatively free of feral colonies.

Limited data also suggest that the densities of feral colonies of honeybees in other countries are typically no more than a few colonies (0.5-8) per km^2 though in some localised areas densities equivalent to over 100 col/km^2 have been recorded (Visscher and Seeley 1982; Roubik 1982a; 1988, 1991; Schneider and Blyther 1988; Danka et at. 1992, 1994).

Differences between feral and managed colonies of honeybees

Feral and managed colonies of honeybees are often assumed to differ in size and resource acquisition as well as in patterns of dispersion. For example, feral colonies are often assumed to be smaller than managed colonies because of the limited capacity of many of the hollows and cavities they use. Consequently on a per hive basis, managed

Table 3 Qualitative information on the distribution of feral colonies of honeybees in Australia.

State	General distribution	Areas with high(est) densities	Areas with low(est) densities	Sources
Tas	throughout		higher altitudes	K Ziegler
				H Ayton
Vic	throughout	NW mallee regions and riparian habitats ironbark woodlands; NE regions; drier woodlands in SW	wetter forests of E Vic	G Arnold
NSW	throughout		alpine areas	G Pyke
SA	throughout	SE remnant woodlands; Murray Mallee; Kangaroo Island; Yorke Peninsula; West Coast	arid interior away from watercourses	D Woodward
		SW regions & coastal plains		D Paton
				G Cotton
				SA Apiarists
				K Spurge
WA	most of state		virtually absent from dry desert country E of Kalgoorlie and N of Geraldton	R Manning
				L Allan.
NT	widespread in low numbers	along water courses; rural habitats near Darwin & Katherine; Douglas-Derby area	patchy in Top End arid areas away from water courses	A Anderson
				B Walsh
				M Fleming
Qld	widespread more likely in eucalypt forests than rainforests	coastal, high rainfall areas; open eucalypt forests and woodlands	Cape York Peninsula	P Arming
				T Bartareau

Table 4 Abundance of feral colonies in locations in SA and Vic. Range of values represent annual fluctuations in numbers of colonies recorded in tle study area. Note that in most cases only small areas have been systematically searched and densities calculated from those studies should be treated cautiously. All data collected by Paton et al. (unpubl.) except for Wyperfeld NP data from Oldroyd *et al.* (1994).

Location	Habitat	Area (ha)	No. of feral colonies	Col/ha
Cromer CP (SA)	open woodland	15	6	0.4
Scott CP (SA)	open woodland	9	1	0.1
Ngarkat CP (SA)	mallee-heath	3600	4	0.001
Mt Rescue CP (SA)	mallee-heath	2000	7	0.004
Flinders Chase NP (SA)	mallee-forest	200	45-80	0.2-0.4
Wyperfeld NP (Vic)	riparian woodland	35	27	0.77

colonies may harvest more floral resources than a feral colony. In addition, beekeepers continually remove surplus honey and pollen from managed hives stimulating increased foraging activity and increased collection of food resources. Beekeepers also regularly shift their hives to new resources when floral resources decline in an area. Consequently the strength of managed hives may be maintained more consistently throughout the year than feral colonies that experience periods of limited floral resources.

Seeley (1985), Thorp (1987) and Winston (1987) provide general information on the sizes of feral colonies of honeybees in North America, where feral colonies ranged in size from 10,000-30,000 bees, occupied nest cavities that ranged in volume from 15-80 L and produced on average 20 kg of honey per year. The cavities used usually had small (<75 cm^2) entrances at the bottom. Feral colonies usually swarmed at least once per year and survival of these swarms was low during the first year (25%) but subsequently high (80%) for those that survived the first year. For comparison, commercially-managed colonies in North America usually consisted of 20,000-60,000 bees, had hives with volumes of 125-250 L and produced 50-100 kg of honey per annum. Survival was high and only about 25% of the colonies in commercial apiaries swarmed each year. Sizes of commercially-managed hives in Australia are similar, with the most productive hives containing at least 40,000 bees (Winn 1972; Turner *et at.* 1972).

North American, South American, European and African statistics for feral colonies are often used to estimate sizes of feral colonies in Australia (Wapshere 1988; Stace 1988; Manning 1989; 1993a; Oldroyd *et al.* 1994). However, there have been no measurements of the sizes of cavities used by feral honeybees in Australia and no measures of the sizes of colonies in terms of total numbers of bees. Some estimates suggest feral colonies may contain as few as 3000-5000 honeybees (J Davies in Wills 1989) yet there are also reports of individual colonies producing comb at least 1.5 m in length (Pyke 1990, Woodward 1993). A colony with a comb of that size would probably contain over 30,000 bees. In part, the lack of information on the sizes of feral colonies in Australia reflects the difficulty of measuring cavities particularly when these are occupied by colonies of bees.

Paton *et al.* (MS2, unpubl.) used a different technique to estimate the size of feral colonies. In parts of Flinders Chase NP they estimated the strength of feral colonies at different times of the year by recording the rates at which honeybees returned to feral colonies at regular intervals (45 min) throughout the day. In this area individual colonies differed in strength by up to 10 fold. Strong colonies had over 60,000 bee returns per day in goodweather during late summer when E. *cladocalyx* was flowering, while weaker colonies managed less than 20,000 bee returns per day. Honeybee activity was lowest in winter when strong hives had 20,000 bee returns' per day and weaker colonies fewer than 2000 bee returns per day. The proportion of bees returning with pollen also varied seasonally and between colonies. Typically 20-50% of the bees that returned had collected pollen, but many of these had also collected considerable volumes of nectar (Paton *et al.* MS2, unpubl.).

The quantities of nectar and pollen carried home by these bees were also measured. For pollen loads this involved removing the hindlegs of pollen-gathering bees, and placing these inn small plastic vials in 1 mL of lactophenol. The pollen present was then identified and counted in a haemacytometer. Nectar loads were determined by gently squeezing the bees and collecting the fluid in capillary tubes. The volume of fluid was then measured and the sugar concentration determined with a 0-90% Otago sugar refractometer. Volumes and concentrations were converted to mg of sugar. The actual net quantities of sugar collected were determined by subtracting the quantities that samples of ⁻ honeybees carried with them when they left the hive from the loads that bees carried home.

During periods of moderate to high flower abundance and suitable weather, feral colonies harvested on average between 100 and 300 g of sugar/day (equivalent to 120-360 g honey/day) in Flinders Chase NP. During winter when flowers were less abundant and weather conditions and ambient temperatures restricted foraging time, colonies harvested as little as 10 g of sugar/day on days when foraging was possible. Some small colonies only harvested about 2 g of sugar on those days. Poorer foraging conditions and more dilute nectar contributed to the lower returns in winter since individual bees returned with smaller volumes (10-11N1) and more dilute nectar

(14-20% sugar wt/wt), equivalent to only 1.5-2.0 mg sugar/load. At other times in the year each bee returned with an average load of 5-9 mg sugar, 13-19 pl at a concentration of 25-36%. These loads are typical of the average loads collected by honeybees in other countries (eg Rinderer *et al.* 1984), though Roubik *et al.* (1986) reported that African honeybees (A. *mellifera scutella)* collected average loads of 30 0 in lowland forest in Panama. Over a year the gross intake for these feral colonies was equivalent to about 40 kg of honey; this is not the surplus available but the total produced and much of it will be consumed by the bees themselves. For example, a honeybee requires about 0.7 mg sugar/h or 15 mg/day (Winston 1987), so a colony of 10,000 bees would need 150 g/day or 55 kg/year. These calculations suggest that the average size of feral colonies in Flinders Chase on Kangaroo Island is less than 10,000 bees (averaged over a year). Comparable figures for managed hives in Australia are not available. However, records are kept on the quantities of honey produced by beekeepers. Since the 1970s the quantities of honey harvested from managed beehives in Australia has averaged around 50-60 kg per year per productive hive (Read 1972; Wills 1989). About 75-80% of the managed hives in Australia are productive (Read 1972). However, when managed properly 180-200 kg can, be harvested per productive hive in a year (Winn 1972; G Cotton pers. comm.). These quantities are typical of the average quantities produced in other countries that range from 50-100 kg per productive hive (eg Thorp 1987). In addition to the quantities of honey harvested from hives an additional 60-80 kg of honey are estimated to be consumed by the colony in a year (Winston 1987). Managed hives, therefore, produce something of the order of 100-200 kg of honey/year and must harvest, on average, between ,300 and 600 g of sugar/day throughout the year. During favourable conditions managed colonies of honeybees will harvest 1-2 kg/day (G Cotton pers. comm.). This rate of intake can be met with about 150, 000 foraging trips, about 3 times the number of foraging trips made by a strong feral colony on Kangaroo Island. Winston (1987) suggests 163,000 foraging trips can be made daily by workers from strong colonies of managed hives. Thus feral colonies do not appear to reach the same size as managed colonies.

Information on the quantities of pollen harvested by feral and managed honeybees in Australia is also limited. According to Winston (1987) estimates of a managed colony's annual requirements for pollen vary from 15 to 55 kg/ year. Given this, managed colonies of honeybees need to harvest 40-150 g of pollen per day throughout the year, and given that some days are not suitable for foraging substantially more than those amounts needs to be harvested when conditions are suitable. The maximum daily intakes that have been recorded for managed hives in Australia has been around 1-1.5 kg of pollen/day during a honey flow on *E. camaldulensis* (Winn 1972; Doull 1973). This is equivalent to about 250, 000 million *Eucalyptus* pollen grains (1 million pollen grains weigh about 5 mg; Doull 1973), or equivalent to the bees harvesting all of the pollen produced by about 500,000 *Eucalyptus* flowers. The amounts of pollen produced by individual flowers of various eucalypts varies from 160,000 to 820,000 pollen grains depending on the species (Paton unpubl.). Five feral colonies in Flinders Chase NP were estimated to collect on average about 20 g of pollen/day but varying through the year from 12 g to 39 g (Paton *et al.* MS2, unpubl.). The strongest feral colony harvested an estimated 105 g of pollen/day when *E. cladocalyx* was flowering (Paton unpubl.). These intakes suggest that feral colonies in Flinders Chase NP, on average, consume about 7 kg of pollen annually and substantially less than that needed by a managed colony. These estimates of pollen harvest suggest that feral colonies are substantially smaller than managed colonies.

Summary

Feral and managed colonies of honeybees have been present in Australia for about 160 years, but their distribution and abundance has increased dramatically over the last 60 years. Information on the current distribution and abundance of feral and managed colonies of honeybees in Australia is limited. There are over 540,000 managed colonies of honeybees in Australia and an unknown number of feral colonies. Managed and feral honeybees are present in all states and territories but are largely absent from alpine areas and from arid inland areas away from water.

Managed colonies of honeybees are patchily distributed in time and space. For example, managed colonies are usually shifted into areas of woodland, forest or heath for 2-4 month periods to exploit flowering peaks of certain plants (often species of Eucalyptus) before being shifted to other areas, including agricultural areas to pollinate horticultural crops. Although around 100 hives are usually _stationed at an apiary at one time, bees from this apiary will forage over an extensive area around this site with individual bees foraging several kilometres from their hives. This reduces the effective density of hives at an apiary to about 0.1 col/ha, a density not dissimilar to the densities recorded for feral colonies.

Feral colonies are also patchily distributed but quantitative data are limited to a few relatively small areas. In those areas densities have been as low as 0.001 col/ha and as high as 0.77 col/ha. The high densities reported in some areas may reflect the localised availability of suitable nesting habitat (hollows) for colonies and not reflect the functional or effective density of colonies in an area as a whole.

Information on the sizes of feral colonies in Australia and on the population dynamics of feral colonies is limited to just one ongoing (and as yet unpublished) study on feral honeybees in Flinders Chase National Park on Kangaroo Island. Feral colonies were present throughout the year in this area and maintained a fairly constant density of 0.3 col/ha. These feral colonies, however, were generally smaller than managed colonies, based on the numbers of foraging honeybees returning to colonies and on the quantities of nectar and pollen that they harvested.

When present in an area a managed colony of honeybees was likely to harvest 3-5 times the quantity of nectar and pollen being harvested by a feral colony.

Considerably more information on the distribution and abundance of both feral and managed colonies of honeybees is still needed but measuring densities alone will not be sufficient to assess the likely effect of honeybees on natural systems. Ideally the distribution and abundance of floral resources that are used by honeybees and the extent to which those resources are limiting to both native fauna and honeybees must also be established. Such assessments should also extend to assessing the availability of nesting sites for feral colonies and whether honeybees compete with any native fauna for these resources as well. The first step in this process involves identifying the native plants and animals that now interact with honeybees.

3. INTERACTIONS BETWEEN HONEYBEES AND AUSTRALIAN BIOTA

The most important aspect of an assessment of honeybees in Australia is their interactions with the Australian flora and fauna. Some information on these interactions and some evidence for competition between honeybees and selected native fauna are available.

Which plants and animals interact with honeybees over floral resources?

Information on the plant species used by honeybees as sources of nectar, pollen or resin are limited to state or regional lists of plant species of economic importance to commercial beekeepers and to a few more detailed community studies. Most states have publications that list those plant species that produce substantial quantities of nectar or pollen that can be profitably exploited by commercial beekeepers (Purdie 1968; Goodman 1973; Clemson 1985; Manning 1992). Species of *Eucalyptus, Melaleuca,* and *Banksia* are usually listed if they are abundant within a particular region and produce reasonable quantities of nectar and/or pollen on a more or less regular basis. Some indication of annual variation in yield is often given. Less prominent plants that provide few resources for honeybees in these regions are not listed.

More detailed community studies reveal that honeybees interact with a large proportion of the plant species present in temperate heathlands and woodlands. In southern parts of South Australia, honeybees have been recorded visiting over 180 native plant species, approximately half of all the plant species examined during their flowering seasons (Paton 1993, unpubl.). These plants came from 34 families and 86 genera. They ranged from small herbs to large trees and included plants that were pollinated by wind, insects, birds and mammals. Bell (1987), van der Moezel *et al.* (1987), Wills (1989) and *Wills et al.* (1990) recorded honeybees foraging at 136 native species from 67 genera

and 30 families in kwongan sandplain areas of WA. This was over 30% of the 413 plant species present in the area, though not all of these species were observed when in flower. Again, wind-, insect- and bird-pollinated plants were visited by honeybees. The methods used in these studies favoured detection of honeybee visits to species that were widespread and/or had substantial floral displays. Some of the less abundant species may not have been surveyed adequately to establish if honeybees visited their flowers.

Information on the use of Australian plants by honeybees in other communities is generally lacking, though G Williams (Aust Museum) holds some unpublished information on a few plants used by honeybees in subtropical coastal rainforests. In other countries, honeybees have been recorded visiting similar numbers of plant species. For example, Villanueva (1984) reported that European honeybees visited 185 plant species in lowland forest and agricultural areas of Veracruz, Mexico and Roubik (1988, 1991) estimated that honeybees harvested pollen from at least 142 plant species at sites in Panama and were probably visiting 25-30% of the flora.

Table 5 lists over 200 Australian plant genera known to be visited by honeybees in Australia. The table is not based on an exhaustive survey but clearly shows that diverse taxa are directly involved in interactions with honeybees. Other plant species may interact indirectly with honeybees if their native pollinators also use plants exploited by honeybees and the behaviour and abundance of native pollinators are altered as a result. No studies have considered those types of interactions in an Australian context (but see Hopper 1987).

There is an equally wide diversity of native fauna that use the same plant species for floral resources as honeybees (Armstrong 1979; Anderson 1989; Wills *et al.* 1990; Pyke 1990; Ettershank and Ettershank 1993; Paton 1993). Knowledge of vertebrate plant

use far exceeds knowledge for invertebrate use. Conservative estimates suggest that thousands of native invertebrates (beetles, butterflies, moths, bees, flies, wasps, ants) now share food resources with honeybees at flowers, as do over 100 species of vertebrates. In many cases specific identities of the insects involved in interactions are not known except in a scattering of studies where insects have been collected and identified (Hawkeswood 1981a,b; Bernhardt *et al*. 1984; Ireland and Griffin 1984; Kenrick *et al.* 1987; *Wills et at.* 1990; Ettershank and Ettershank 1993; O'Brien and Calder 1993; Paton and Jansen unpubl., G Williams unpubl.).

Although not well documented many of the species of animals involved in these interactions harvest floral resources from a variety of different plant species (Paton and Ford 1977; Armstrong 1979; Bernhardt and Walker 1984; Bernhardt *et at.* 1984). These qualitative observations indicate that a great diversity of Australian plants and animals interact with honeybees by sharing floral resources. This diversity greatly complicates any assessments of impacts of honeybees. In assessing impacts of - honeybees in an area a representative selection of plant and animal species should be studied. Whether these interactions are harmful will depend on whether resources are limiting and what share of the resources are consumed by honeybees.

Table 5 *List* of *Australian plant genera visited* by honeybees. Genera shown in *bold provide* significant quantities of floral resources to commercial apiaries.

Family	-Genera
Aizoaceae	*Carpobrotus, Disphyma*
Amaranthaceae	*Ptilotus*
Anacarcdiaceae	*Euroschinus*
Apiaceae	*Trachymene*
Araliaceae	*Schefflera*
Arecaceae	*Archontophoenix*
Avicenniaceae	***Avicennia***
Campanulaceae	*Wahlenbergia*
Casuarinaceae	***Allocasuarina; Casuarina,***
Chenopodiaceae	*Halosarcia, Rhagodia*
Chloanthaceae	*Pityrodia*
Cornpositae	*Brachycome, Calotis, Olearia, Podotheca, Senecio, Sonchus*
Convolvulaceae	*Calystegia*
Cruciferae	*Lepidium*
Cunoniaceae	*Ceratopetalum*
Cyperaceae	*Cyperus, Mesomelaena, Lepidosperma*
Dillenaceae	*Hibbertia*
Droseraceae	*Drosera*
Ebenaceae	*Diospyros*
Eleaocarpaceae	*Eleaocarpus*
Epacridaceae	*Acrotriche, Andersonia, Astroloma, Brachycoma, Epacris,* **Leucopogon,** *Styohelia, Woollsia*
Escalloniaceae	*Cuttsia*
Eucryphiaceae	*Eucryphia*
Euphorbiaceae	*Adriana, Bertya, Beyeria, Micrantheum, Phyllanthus, Ricinocarpus*
Flacourtiaceae	*Scolopia*
Frankeniaceae	*Frankenia*
Geraniaceae	*- Geranium, Pelargonium*
Goodeniaceae	*Brunonia, Dampiera, Goodenia, Scaevola, Velleia*
Gyrostemonaceae	*Gyrostemon*
Haemodoraceae	*Anigozanthos, Conostylis*
Haloragaceae	*Glischrocaryon, Gonocarpus, Myriophyllum*
Hypoxidaceae	*Hypoxis*
Iridaceae	*Orthrosanthus*

Juncaceae	Juncus
Labiatae	Ajuga, Hemiandra, Pros tanthera, Westringia
Lecythidaceae	Planchonia
Leguminosae	**Acacia,** Aotus, Bossiaea, Cissus, Clianthus, Crotalaria, Daviesia, Derris, Dillwynia, Eutaxia, Gastrolobium, Glycine, Gomphlobium, Goodia, Hardenbergia, Jacksonia, Kennedia, Mirbelia, Oxylobium, Phylotta, Platylobium, Psoralea, Pultenaea, Senna, Swainsona, Templetonia, Viminaria
Liliaceae	Blandfordia, Bulbine, Burchardia, Caesia, Chaemescilla, Dianella, Dichopogon, Lomandra, Tricoryne, Thysanotus, Xanthorrhoea
Loganiaceae	Logania
Loranthaceae	Amyema, Lysiano, Nuytsia
Lythraceae	Lythrum
Malvaceae	Alyogyne, Lavatera, Sida
Melastomataceae	Melastoma
Meliaceae	Melia
Myoporaceae	Eremophila, Myoporum
Myrsinaceae	Aegicerus
Myrtaceae	Acmena, Agonis, **Angophora,** Baeckea, Beaufortia, Callistemon, Calothamnus, Calytrix, Chamelaucium, Darwinia, Eremaea, **Eucalyptus,** Eugenia, Hypocalymma, Kunzea, Leptospermum, **Melaleuca,** Micromyrtus, Rhodomyrtus, Scholtzia, Syncarpia, Syzigium, Thryptomene, Trystaniopsis, Verticordia, Waterhousea, Xanthostemon
Onagraceae	Epilobium
Orchidaceae	Dendrobium, Diurus, Drakaea, Eriochilus, Prasophyllum
Oxalidaceae	Oxalis
Phytolaccaceae	Tersonia
Pittosporaceae	Billardiera, Bursaria, Cheiranthera, Pittosporum
Polygalaceae	Comesperma
Polygonaceae	Muehlenbeckia
Primulaceae	Samolus
Proteaceae	Adenanthos, **Banksia,** Cardwellia, Conospermum, **Dryandra,** Grevillea, Hakea, Isopogon, Lambertia, Macadamia, Persoonia, Petrophile, Stenocarpus, Synaphea, Xylomelum
Ranunculaceae	Clematis, Ranunculus
Rhamnaceae	Alphitonia, Cryptandra, Pomaderris, Spyridium, Ventilago
Rosoceae	Rubus
Rutaceae	Acradenia, Baronia, Correa, Diplolaena, Eriostemon, Flindersia, Geljera, Phebalium, Zieria
Santalaceae	Choretrum, Leptomeria, Santalum
Sapindaceae	Alectryon, Atalaya, Dodonaea, Guioa
Scrophulariaceae	Euphrasia, Derwentia, Stemodia
Smilaceceae	Smilax
Solanaceae	Anthocercis, Solanum
Stackhousiaceae	Stackhousia
Sterculiaceae	Argyrodendron, Brachychiton, Guichenotia, Keraudrenia, Lasiopetalum, Thomasia
Stylidiaceae	Stylidium
Surianaceae	Stylobasium
Thymelaeaceae	Pimelea
Umbelliferae	Actinotus, Apium, Hydrocotyle
Violaceae	Hybanthos, Viola
Winteraceae	Tasmania
Zygophyllaceae	Zygophyllum

Sources: Adams and Lawson 1993; T Bartareau pers. comm.; Bell] 987; Bernhardt et al. 1984; Clarke and Myerscough 1991; Clemson 1985; Ettershank and Ettershank 1993; Goodman 1973; Gross 1993; Heard 1993; Hopper 1 980b, 1987; Lamont 1985; Manning 1992; Paton and Jansen unpubl.; Purdie 1968; Pyke and Balzer 1985; van der Moezel et al. 1987; G.Williams pers. comm.; Wills 1989; Wills et al. 1990.

Prominence of honeybees at flowers of Australian plants

Three types of data provide information on the prominence of honeybees at flowers of Australian plants:

1. collections of insects from flowering plants;
2. counts of insects at flowers; and
3. observations on the frequency of visits by animals to flowers.

Counts and collections of insects from flowers show that honeybees may account for more than half the insects using the flowers of many plant species (table 6). These collections and counts only estimate the numbers of each taxon that are foraging at a particular time and do not consider differences between taxa-in the speed at which they can visit and shift between flowers. Observations on the number of visits to flowers reveal that flowers are often visited several times a day by honeybees and that honeybees often accounted for more than half of all visits to many flowers (table 6). Given this, honeybees could remove a large share of the floral resources from Australian plants and so potentially compete with native flower -visiting fauna.

Table 6 Prominence of honeybees at the flowers of Australian plants. Data provided in the table illustrate that honeybees are often the most prominent visitors to the flowers of a wide range of Australian plants.

Plant species	Honeybee visits to flowers		Other taxes visiting flower	Source
	of specimens, counts or visits'	visits/flower/dayb		
NSW				
Grevillea x gaudichaudii		>26.4' (> 0.78)	bd	Taylor & Whelan 1988
Pultenaea elliptica	12 (c)			Pyke & Balzer 1985
Eucalyptus gummifera	68 (c)		nb,?bd	"
Hakea teretifolia	60 (c)		nb	"
Leptospermum squarrosum	92 (c)		nb,?bd	"
Angophora hispida	66 (c)		n b	"
Banksia ericifolia	25-58 (v)	12-155'	a,bd,m,nb	Paton & Turner 1985
Banksia spinuloso	0-66 (v)	0-12.0'	bd	Vaughton 1992
Vic				
Grevillea aquifolium	72 (v)	20.1	bd	Paton 1985
Callistemon rugulosus	95 (v)	77	bd	Paton 1979
Amyema pendulum	62 (v)	18.1	bd	"
Tas				
Eucryphio spp	19-48 (s)		ins	Ettershank & Ettershank 1993
SA				
Eucalyptus cosmophylla	23-66 (v)	2.8-54.6	bd,nb	Paton 1990
Eucalyptus remotes	57 (v)	9.2	bd,nb	"
Callistemon rugulosus	38-94 (v)	5.4-13.1	bd	"
Adenanthos terminalis	0-98 (v)	0.0-5.1	bd	"
Acacia paradoxes	44-97 (v)	1.2-10.9h	nb	Paton *et al.* MS2
Banksia marginata	67-92 (v)	22.9-128.3'	bd,nb	"
Conospermum patens	13-77 (v)	0.3-1.3	nb,ins	"
Dorwinia micropetala	2-40 (v)	0.5-8.2	nb,ins	"
Daviesia genistifolia	77 (v)	5.5	nb	"
Eucalyptus baxteri	32-74 (v)	4.3-8.4	bd,nb, ins	"
Grevillea parviflora	>83 (v)	13.4	nb	"
Hakea rostrato	>75 (v)	13.3	nb, ins	"
Leucopogon parviflorus	52-86 (v)	1.6-2.7	nb -	"
Melaleuca gibbosa	39-53 (v)	7.4-39.9	nb,ins	"
Orthrosanthus multiflorus	>36-1 00 (v)	13.8-62.3	nb	"
Phyllota pleurandroides	22-96 (v)	1.1-10.7	nb,ins	"

Species	Visits	Nectar	Visitors	Reference
Pimelea flava	67-100 (v)	1.3-3.7	nb,ins	"
Prostanthera spinosa	7-81 (v)	0.3-0.8	nb,ins	"
Pultenaea viscidula	86 (v)	14.2	nb	"
Swainsona lessertifolia	91-100 (v)	4.623.1	nb	"
Xanthorrhoea semiplana	84 (v)	1.7	nb,ins	"
Hibbertia virgata	75-79 (c)	16.8-21.4	a,bt,m,s	Paton unpubl.
Eucalyptus fasciculosa	18 (c)	2.4	a,bt,f	"
Acacia *myrtifolia*	86 (c)	2.1 h	nb	"
Acacia pycnantha	100 (c)	1.9h		"
Dillwynia sericea	50 (c)		nb	"
Brachyloma ericoides		14.9	bd	"
Pultenaea canaliculata	85-96 (c)		nb,ins	"
Pultenaea tenuifolia	48-56 (c)		nb,ins	"
Pimelea glauca	0-89 (c)		ins	"
Pimelea humilis	0-33 (c)		ins	"
Calytrix tetragona	0-100 (c)		ins	"
Dampiera marifolia	63-100 (c)		ins	"
Dampiera rosmarinifolia	82-100 (c)		ins	"
Eutaxia microphylla	0-94 (c)		nb,ins	"
Eucalyptus odorata	81 (c)		bd,nb, ins	"
Dillwynia hispida	11 -100 (c)		nb,ins	"
Scaevola aemula	53-100 (c)		ins	"
Lasiopetalum baueri	0-94 (c)		ins	"
Acacia calamnifolia	0-75 (c)		ins	"
Daviesia benthami	13-14 (c)		nb, ins	"
WA				
Calothamnus quadrifidus	74 (v)	-25	bd	Collins *et al.* 1984a

(a) c = counts; s = specimens; v = visits(b) i = visits per inflorescence per day; h= visits per flower head per day; all others

are visits per flower per day(c) a= ants; bd = birds; bt = beetles; f = flies; m = moths; nb = native bees; s= syrphid flies; ins = insects

Availability and consumption of floral resources

The beekeeping industry defends its periodic use of natural resources by arguing that beekeepers only exploit surplus resources during flowering •peaks and so have little effect on natural processes. Feral colonies on the other hand are more likely to affect natural processes because they remain in an area throughout the year, including lean periods when more intense competition for floral resources may exist. This argument suggests that in many natural systems there are periods in the year when the amount of nectar being produced is substantially higher than at other times and that native fauna are unable to fully consume these peaks in resource production.

Floral resources in Australian ecosystems have rarely been measured except for the quantities of nectar available to nectar-feeding birds in a range of heathland and woodland sites in southern Australia (Ford 1979; Paton 1979, 1985, 1986; McFarland 1986a,b; Ford and Paton 1982; Pyke 1983, 1985; Newland and Wooller 1986; Collins and Newland 1986). In most of these areas there were substantial seasonal variations in the quantities of nectar being produced. For example in coastal Banksia heathlands near Sydney production varied 10-100 fold throughout the year, averaging 1-10 g sugar/ha/day during summer and around 100 g sugar/ha/day for 2-3 months over winter when B. ericifolia was flowering (Pyke 1983; Pyke and Recher 1986). Similarly production of nectar in an area of open forest with an understorey of Banksia spp in New England NP varied from effectively 0 g/ha/day during summer to 1125 g sugar/ha/day for 2-4 months during late winter and early spring although from one day to the next the amounts produced in winter varied dramatically (Ford and Pursey 1982; McFarland 1986a,b). In Banksia dominated heaths and swamps in South Australia and Western Australia nectar production also peaked for 2-3 months during winter at 200-1000 g sugar/ha/day depending on the location (Newland and Wooller 1986; Paton et at. MS3, unpubl.).

In other areas without a dominance of *Banksia,* like the Royal Botanic Garden's Annexe at Cranbourne, Victoria, nectar production varied from 12-30 g sugar/ha/day throughout the year as different plants came in and out of bloom (Paton 1979, 1986). In woodland areas near Horsham nectar production usually varied from 10-100 g sugar/ha/day but for short periods of time when certain eucalypts flowered productivities approached 375 g sugar/ha/day (Paton 1985). The eucalypts, however, did not flower reliably in each year. Heathy woodlands adjacent to *Banksia* swamps in WA produced 10-50 g sugar/ha/day and woodland areas adjacent to *Banksia* heathlands near Sydney produced from 0-225 g sugar/ha/day with peaks in productivity in these habitats not coinciding with those in the adjacent *Banksia* habitats (Pyke 1985; Newland and Wooller 1986). Production of nectar in Jarrah forests in WA varied seasonally from close to 0 g/ha/day in late summer to around 150 g sugar/ha/day in late spring when *B. grandis* flowered (Collins and Newland 1986).

In most of these studies attempts were made (with mixed success) to correlate the numbers of honeyeaters and their calculated energy requirements with the quantities of nectar being produced (Paton 1979, 1985; Ford 1983; Ford and Paton 1985; Pyke 1983, 1985, 1988; Pyke and Recher 1986; McFarland 1986a,b; Newland and Wooller 1986). In some areas there was a close match between the quantities needed to support native fauna and the quantities being produced. However, in other areas at certain times in the year, particularly winter, the production of nectar was higher than that needed to support the populations of native nectar-feeding birds in those areas, suggesting that surpluses do exist at least in some areas in winter.

The notion that surpluses sometimes exist is further supported with observations of nectar dripping from flowering inflorescences of some banksias during winter months. Various hypotheses for this phenomenon have been proposed (eg Carpenter 1978). Such surpluses, however, may be caused by a lack of visitation by native pollinators (mainly birds) rather than excessive production by the plants. In most cases the rate of production on a per inflorescence basis is moderate and averages about

0.2-1 g sugar/inflorescence/day depending on the species (Ford and Pursey 1982; Ford and Paton 1982; Paton and Turner 1985; Paton 1986, unpubl.; McFarland 1985; Pyke 1983, 1988). Suggestions that a *B. ornata* inflorescence can shed over 300 ml of nectar (ca 60 g sugar) in less than a day are, however, inconceivable (Berkin 1987).

These periods of resource surpluses are sometimes used to argue that populations of honeyeaters are not limited by floral resources and that honeybees pose no threat to nectar-feeding birds (Stace 1988; Manning 1993a). However, this selectively ignores other studies that showed the numbers of birds to be closely linked to the production of floral resources and to the proportion of those resources that the birds could harvest (Paton 1979, 1985).

There are of course a range of possible interpretations for the existence of surpluses at certain times in the year. One is that population densities of birds may be limited by the availability of nectar at other times in the year such that their numbers could never reach the carrying capacity of the winter resources. The imbalance could arise from differential clearance of summer habitats relative to winter habitats but could equally be induced by heavier losses of resources to honeybees during the warmer months. Paton (1985) showed that consumption of nectar resources by honeybees was higher during the warmer months of the year than during winter.

In summary, studies have found that surplus floral resources do exist and more in-winter than at other times in the year. However, these studies have been largely restricted to heathlands or low woodlands where understorey plants produce most of the nectar over winter, and to areas supporting reasonably high populations of honeyeaters. As such these studies may not be representative of-other areas. Furthermore, in most cases resources were only assessed over small selected areas (a few hectares) and the results may not extrapolate to estimate nectar production over more extensive areas.

The production of floral resources by eucalypts has largely been neglected in all of these studies, reflecting the difficulty of measuring floral resources produced by tall trees. Paton (1986) reported that nectar production by several species of eucalypts

ranged from 0.5 to 25 mg sugar/flower/day and from 2 to 85 g sugar/tree/day with the most productive species being *E. leucoxylon.* Ironbark *(E. sideroxylon)* may produce even greater quantities of nectar. For example, Damon Oliver (pers. comm.) estimated that individual flowers produced about 15 mg sugar/day, and that individual trees could produce 200 g sugar/day with ironbark forests (ca 100 trees/ha) producing 20 kg sugar/ha/day. Given this, periods of resource surpluses may also exist when certain eucalypts are flowering but as yet there have been no quantitative measurements.

For comparison some rough estimates of the quantities of floral nectar harvested by commercial apiaries suggest that during a moderate to high honey flow an apiary of 100 hives produces about 6 tonnes of honey during a 3 month period of which about 4 tonnes would be removed by the beekeeper (eg Manning 1993b). This is equivalent to each hive collecting about 60 kg of honey, or 50 kg of sugar (honey is about 85% sugar and 15% water) during a 3 month period or about 500 g sugar/day. Assuming that these bees forage predominantly within 2 km of their hives (a reasonable assumption if occupied apiary sites are on average 4 km apart) then these honeybees would be harvesting about 50 g sugar/ha/day assuming the apiary was completely surrounded by suitable habitat. Although crude, these rates of harvest can be met by the quantities of nectar being produced during peak flowering periods in some habitats.

A second method has been used to assess nectar availability in some of these bird-plant systems. These assessments have involved measuring the quantities of nectar remaining in flowers at various times during the day and comparing these to either the energetic costs of the birds to harvest those resources or to the quantities in bagged flowers (Ford 1979; Paton 1979, 1982a, 1985; Collins *et at.* 1984a,b; McFarland 1986a; Collins and Newland 1986; Armstrong 1991). These studies found that for some plant species there was little change in the quantities of nectar available at flowers throughout the day and that the energetic returns for honeyeaters to harvest those resources remained high throughout the day. Such occasions, however, were more frequent during winter months consistent with earlier

findings of winter surpluses in other plants. At other times, notably the warmest months, the energetic returns to honeyeaters for feeding on nectar were at best only marginally profitable for much of the day. Under such conditions, honeyeaters were often territorial around the densest clumps and/or most productive flowers, indicative of limited food resources (Paton 1979, 1985; Ford 1979, 1981).

A third approach to assessing resource availability has been to calculate the proportion of floral resources that are being consumed by different floral visitors at selected plants. Most studies have only considered the quantities of nectar being consumed by different floral visitors at plants largely pollinated by birds. At these plants honeybees consumed 14-97% of the nectar being produced (Paton 1979, 1985, 1990; Bond and Brown 1980; Collins *et at.* 1984a; table 7). In most cases birds began foraging earlier in the day than honeybees. At these times nectar levels in flowers were often much higher than later in the day and so honeyeaters gained a dis-proportionate share of the resources relative to their daily visitation rates. Paton (1990) also considered the fate of pollen at some of these plants and found that honeybees removed 39-99% of the pollen being produced (table 7).

Similar calculations are still to be made for a range of insect-pollinated flowers. However, the proportion of resources consumed by honeybees will be similar to or higher than the proportion of visits being made by honeybees to the insect-pollinated flowers listed in table 6 for two reasons. First, honeybees usually begin foraging 1-2 hours earlier than native insects at least in temperate locations (eg Paton 1993) and so have more or less exclusive use of these flowers at times when nectar and pollen availability are highest (Paton unpubl.). Second, honeybees being larger than most of the native insects visiting these flowers, usually remove more nectar or pollen during a visit to a flower than the native insects (Paton unpubl.). Given that honeybees often accounted for 80% or more of the visits to flowers of a wide range of insect-pollinated plant taxa (table 6) their share of the floral resources will be at least this high. Therefore, interactions between honeybees and Australian biota are not trivial and the potential for competitive interactions is high. These measurements alone, however, do not

Table 7 Quantities of nectar and pollen removed by honeybees and native fauna visiting plants near Rocky River in Flinders Chase NP, SA. Sets of data illustrate temporal variation in resource use. HB = honeybees; BD = birds; NB = native bees; % resource removed = percentage of nectar and pollen produced that was taken by each taxon; + _ < 0.001. Further details in Paton (1990).

Plant species	Months	% resource removed		
		HB	BD	NB
NECTAR				
Eucalyptus cosmophylla	mid Aug 87	14.1	85.8	0.1
E. cosmophylla	late Aug 87	29.9	70.0	0.1
E. remota	Jan 89	16.1	83.7	0.2
Callistemon rugulosus	Nov 88	40.9	59.1	
C. rugulosus	Dec 88	92.1	7:9	
Adenanthos terminalis	Aug 87		100.0	
A. terminalis	Jan 89	97.2	2.8	
POLLEN				
Correa *reflexa*	May 87	38.7	61.3	
C. reflexa	Jul 87	75.9	24.1	
C. reflexa	Aug 87	93.1	6.9	
E. remota	Jan 89	88.0	12.0	+
A. terminalis	Aug 87		100.0	
A. terminalis	Jan 89	99.0	1.0	

Bond and Brown (1979) estimated honeybees consumed 13-20% of the nectar produced by E. *incrassata* at Wyperfeld NP, Vic in Oct-Nov *1977 and Collins et al. (1984a) estimated honeybees consumed 39% of the nectar produced by Calothamnus quadrifidus in Nov 1983 at* Wongamine Nature Reserve, WA. Honeybees also consumed 36% of the nectar produced *by Grevillea aquifolia* at Golton Vale, central Vic in Oct *1977, 52% of the nectar produced by Callistemon rugulosus* at Golton Vale in Nov 1977, and 34% of the nectar produced by Amyema *pendulum* at Cranbourne, Vic in Nov 1977 (Paton 1979, 1985). In each example honeyeaters either consumed or were assumed to consume the remainder.

provide evidence of competition, since honeybees could still be removing floral resources that were not needed by native fauna.

Competition between honeybees and native fauna for floral resources

A number of studies have attempted to show experimentally that honeybees compete with some native fauna for floral resources. These experiments have involved manipulating the numbers of honeybees in an area-usually by adding beehives to a site-and measuring responses of selected native fauna-usually native bees or honeyeaters.

Effects of honeybees on numbers of native bees

Pyke and Balzer (1985) conducted the first manipulative studies. In 1981 and 1982 they manipulated the numbers of honeybees working flowers used by native bees and recorded responses of native bees to these manipulations. In their first experiment they selected eight 1 m² plots of *Leptospermum squarrosum*. Four of these plots acted as

controls and the other four were' experimental plots. At the experimental plots honeybees were removed on six days between 1 and 17 April 1981. On these days they repeatedly counted the numbers of honeybees and native bees arriving at these census plots for ten minute periods. About four counts/plot/day were made. These counts were then compared with counts collected at the same plots on four days when honeybees were not removed. Both sets of data were also compared with similar data collected at the four control plots where honeybees were not removed on any of the days. More native bees arrived at the experimental plots for those days when honeybees were being removed (table 8) and Pyke and Balzer interpreted this response as indicating a competitive interaction. However, there were still large numbers of honeybees arriving at the experimental plots on these days and the rates of arrival were similar to the numbers arriving at control plots (table 8). Pyke and Balzer (1985) did not state whether the honeybees that arrived during counts at experimental plots on days when honeybees were to be removed were allowed to forage. However, elsewhere in their report (see table 5.1 in Pyke and Balzer 1985), they recorded

the time taken by honeybees to visit flowers within these experimental plots on removal days, so at least a proportion of these honeybees must have foraged. The availability of floral resources may not have been very different in the experimental and control areas, since the proportion of floral resources removed by honeybees is not necessarily proportional to the numbers of honeybees foraging in an area (eg Paton 1990).

Table 8 Mean arrival rates of honeybees and native bees per hour at 1 m^2 plots of *Leptospermum squarrosum* on days when honeybees were removed (-HB) and not removed (+HB) from experimental plots (Pyke and Balzer 1985). Standard errors were approximately 10% of the means for honeybees (1.8 to 3.2) and 15-50% of the means for native bees (0.8 to 1 .5).

	Honeybees		Native bees	
	+HB	-HB	+HB	-HB
Experimental plots	38.5	23.0	3.4	10.0
Control plots	19.7	17.3	2.1	4.4

An implicit assumption in this study is that native bees can detect differences in the availability of floral resources at a scale of 1 m^2 . If they are unable to detect such differences then there is no a priori reason to expect their numbers to increase in experimental plots when some of the honeybees have been removed. Other factors like the densities of flowers in the various plots and adjacent to them rather than the numbers of honeybees arriving at the plots may have influenced the arrivals of native bees. Unfortunately information on the numbers of flowers at control and experimental sites were not given although these were counted at least for the first day. Other pertinent details were also not given. For example, no᾿ information was given on the numbers of honeybees that were removed from each plot, the timing of this removal relative to the counts, or the spatial arrangement of the eight plots although these were all within an area of 100 m^2. Given the proximity of the experimental and control plots, removal of honeybees from experimental plots may have also influenced the numbers using nearby control plots. Furthermore, the numbers of arrivals of bees may not be a good measure of insect activity at flowers within the plots. Ideally the length of each visit (ie numbers of flowers probed within the 1 m^2 plot) not just the number of

visits (arrivals) should be recorded. Low rates of arrival may have been countered by lengthy stays. Without some of this additional information interpreting an apparent increase in the numbers of native bees at the 1 m^2 experimental plots in response to removing some of the honeybees as evidence of competition between honeybees and native bees is difficult.

Bailey (1994) reports more convincing results following similar removal experiments conducted near Jandakot, WA during autumn when floral resources were scarce. In the study, the numbers of insects attending flowering *Leucopogon propinquus* plants were counted for repeated 30 min periods between 1130 am and 1515 pm for three days when honeybees had access and for three days when honeybees were being removed. On days when feral honeybees were being removed the numbers of two species of native bee, *Campsomeris sp.* and *Nomia sp.* increased as did an unknown species of Diptera. Other native insects were also recorded but their abundances were too small and. variable to detect any significant changes following removal of honeybees.

Pyke and Balzer (1985) also counted the numbers of honeybees and native bees arriving at 1 m^2 plots of *Angophora hispida* at four distances away from a permanent apiary of 60 hives in Royal National Park near Sydney. They suggested that a decrease in honeybee density (arrivals), and an increase in native bee density, with increasing distance from the apiary would be indicative of a competitive interaction between honeybees and native bees. Such a pattern was not found. The numbers of both honeybees and native bees visiting plots of *Angophora* flowers were highest at the furthest distance (800 m) from the apiary at which Pyke and Balzer collected data. The notion that there should be a decline in honeybee activity with distance from an apiary may not always hold. For example, Visscher and Seeley (1982) found that foraging honeybees were often patchily distributed by distance and direction from their hives and that the dispersion patterns of foraging honeybees often changed dramatically from one time period to the next. In addition the densities of honeybees foraging in different plots in Royal NP may have been influenced by the distribution and abundance of feral colonies.

Pyke and Balzer (1985) also introduced 30 hives of honeybees to an alpine area of Kosciusko NP where there had been no previous history of honeybees. Responses of native bees to this introduction were measured at four distances from the apiary by counting the numbers of bees seen along transects and the numbers arriving at 1 m^2 census plots of flowering *Prostanthera cuneata* before and after the introduction of the hives. The two sets of data provided some interesting contrasts. Both transect data and arrival data showed that honeybee densities were greatest at sites close to the apiary than at sites further away (table 9). Transect counts also showed that native bee densities were consistently higher close to the apiary (50 m) than further away both before and after the arrival of honeybees (table 9). At sites 1000 m from the apiary the densities of native bees remained low and did not change dramatically following the introduction of honeybees. At sites closer to the' apiary the densities of native bees declined following the introduction of honeybees. At sites 50 m from the apiary the density was halved but at sites 200 m and 400 m from the apiary densities of native bees were only 10-20% of the prehoneybee counts. If honeybees were competing with native bees for floral resources then the declines should have been more severe at sites closest to the apiary where honeybee densities and activity was highest (approximately 4 times higher than at other distances).

Counts of native bees arriving at census plots, however, did not mirror counts of native bees along transects (table 9). No explanation was given for these differences. Although counts of native bees arriving at census plots declined close to the apiary they still remained high relative to areas further from the apiary. If honeybees were competing with native bees for resources then native bees might be expected to avoid areas with

the highest honeybee densities. This was clearly not the case.

The inconsistencies between the two methods for censusing native bees weakens Pyke and Balzer's claim that these experimental data provide evidence of competition. A variety of abiotie factors (eg temperature, wind, time of day, cloudiness) are likely to influence foraging activities of native bees (eg Paton 1993) and ideally simultaneous counts should have been made in the various areas to allow valid comparisons. Pyke and Balzer (1985) gave no details on when different areas were sampled with each of the two techniques or whether each area was sampled under comparable weather conditions. Slight differences in ambient conditions from one day to the next, from one location to another (eg east- and west-facing slopes) and from one time interval to the next within a day could have influenced the activities of native bees when counts were made, and so produced the patchy and inconsistent sets of results. Pyke and Balzer unfortunately did not consider these possibilities when designing their sampling program and only censused bees in one direction away from the apiary.

Other difficulties potentially exist with these data. For example, Pyke and Balzer (1985) provided few details on the species of native bees and other taxa that were recorded in plots or along transects before and after the honeybee manipulations and how the counts for each species of native bee and other taxa varied spatially and temporally. Identification to species, however, is often difficult without microscopic examination of the individual bees and so that is an understandable omission.

In conclusion, Pyke and Balzer (1985) have not provided convincing evidence of competitive interactions between honeybees and native bees but nor have they shown that

Table 9 Numbers of honeybees and native bees counted along 10 m sections of transects and in 1 m^2 plots of *Prostanthera cuneata* at different distances from an apiary of 30 hives stationed in Kosciusko NP. Data are from before and after the introduction of the hives (Pyke and Balzer 1985) .

Distance from	Honeybees				Native bees			
	transects		plots		transects		plots	
apiary (m)	before	after	before.	after	before	after	before	after
50	0.0	0.4	0.0	4.1	0.25	0.11	2.60	0.09
100	0.0	0.1	0.0	1.2	0.19	0.01	0.90	0.00
400	0.0	0.1	0.0	0.3	0.27	0.04	0.00	0.03
1000	0.0	0.02	0.0	0.02	0.04	0.06	0.00	1.30

competitive interactions are non-existent. Rather their work illustrates the paucity of good ecological data on the foraging ecology of Australian native bees and highlights the complexity of interactions between honeybees and native bees. It is a starting point for further studies.

This lack of knowledge and complexity is easily illustrated. For example, the usual assumption is that if honeybees compete with native bees for floral resources then the numbers of native bees counted at a patch of flowers should decline following the introduction of honeybees (Pyke and Balzer 1985; Pyke 1990); honeybees simply displace native bees from flowers. Paton (1993), however, suggested that in a competitive environment the numbers of native bees recorded foraging in an area might actually increase rather than decrease following the introduction of honeybees, reflecting a reduction in the quantities of floral resources encountered at flowers.

This may be the scenario. Female native bees collect nectar and pollen, and package that food with an egg in a chamber or cell within a nesting burrow and then repeat this procedure (Michener 1970). Assume that there are 100 female bees in an area and that the bees take 5 minutes to collect a load of nectar or pollen before returning to their burrows. Once in the burrow, they take 10 minutes to unload before going out to forage again. Now introduce honeybees that remove a large proportion of the nectar and pollen produced in the area. As a result, native bees find less food at each of the flowers they visit and consequently spend more time foraging to obtain a full load. To simplify the calculations assume that under the new conditions with honeybees present a native bee takes twice as long (10 minutes) to collect a load before returning to her burrow. Because unloading still takes 10 minutes, the net effect of introducing honeybees might be to increase the numbers of native bees working flowers at one time. In the example given here the numbers of native bees foraging simultaneously would have risen from 33 to 50, despite the actual numbers living in the area remaining at 100. Thus changes in the numbers of native bees counted at patches of flowers following the introduction of honeybees are not easily interpreted, except that changing numbers indicate some interaction.

Effects of honeybees on the reproductive performances of native bees

Ultimately impacts of honeybees on native bees should result in long term reductions in the population densities of native bees. Three studies have attempted to measure the influence of honeybees on the reproductive performances of some species of native bees. All three studies have involved adding hives to areas where there were also background feral colonies followed by measuring the reproductive performances of a particular species of native bee in areas with and without these added hives. Only one of these studies has been published.

Sugden and Pyke (1991) measured the population biology and reproductive performance of *Exoneura asimillima* in areas where they had introduced beehives and compared these to similar measurements made in control areas 7-8 km away (outside the flight range of the introduced hives). In the first year of measurements the only differences were significantly more large larvae and pre-pupae within the colonies near the apiary than at the control sites and this difference was dismissed as being a possible artefact of sampling colonies near the apiary two weeks after those at control areas. As a result colonies near the apiary may have been more advanced and so had more larvae and pre-pupae. In the second year more founder colonies established near the apiary and these had more eggs, larvae and pre-pupae than founder colonies at the control sites (table 10). Survival of both established and founder colonies was similar at both control and experimental sites. However, there were fewer adults of both sexes in the established colonies at the experimental sites (near apiary) compared with the control sites (table 10). These data are difficult to interpret, particularly given that possible differences in floral resources and microchmates may have existed between sites, and accounted for differences in the composition of colonies between sites (Sugden and Pyke 1991). Unfortunately these experiments were not replicated, and although there were eight experimental plots these were all at the one experimental site and so these other factors cannot be eliminated. Information on the variability between plots in the composition

of colonies is also not given. Nevertheless, the authors interpreted these data to imply a negative effect of honeybees on local colonies of *E. asimillima.* This conclusion was based largely on the lower numbers of adults remaining at established colonies near the apiary.They suggested that competition for food, especially nectar, was possible since honeybees altered the foraging patterns of *E. asimillima* but provided no details. Despite the lower numbers of adults remaining at established colonies, these colonies and founder colonies were at least as fecund if not more so near the apiary than they were at control sites further away and at a larger number of new colonies founded in the experimental sites. Such a result is not consistent with the notion that the bees were competing with honeybees for floral resources. Other possibilities suggested by Sugden and Pyke (1991) were second order interactions where honeybees affected the foraging behaviour, of predatory ants and/or parasites of *E. asimillima* which in turn influenced *Exoneura* colonies.

Two other studies have been measuring the effect of honeybees on the reproductive biology of native bees. Schwarz, Kukuk and Gross (pers. comm.) measured the reproductive performances of *Exoneura bicolor* in control and experimental areas in Cobboboonee State Forest near Portland, Victoria. Four control and four experimental areas were established with experimental areas receiving additional hives of honeybees. These areas had a low background level of feral honeybees (M Schwarz pers. comm.). Initial measurements have revealed that colony survival and brood production were higher in areas where hives had been placed. This result is not consistent with a direct competitive effect of honeybees on *Exoneura.* Kukuk and Schwarz have suggested three possible explanations for these results:

1. subtle differences in resource availability between sites with and without added hives of honeybees such that sites with additional honeybees were still better for *Exoneura;*
2. high honeybee densities leading to the competitive exclusion of some other floral visitor(s) which would otherwise have appropriated a large proportion of the floral resources, leaving more food available for *Exoneura;* and

3. high honeybee densities leading to satiation or prey specialisation by insectivores that would otherwise have preyed on *Exoneura.*

Various predatory ants (eg species of *Myrmecia)* are often seen amongst the flowers of plants waiting to grab unsuspecting insects probing flowers (D Paton pers. obs.; M Schwarz pers. comm.). In Flinders Chase NP most of the insects caught amongst flowers by these ants were honeybees that responded more slowly than native bees to an approaching ant (D Paton pers. obs.). Spessa and Schwarz (pers. comm.) are also measuring the reproductive performances of a native colletid bee *Amphylaeus morosus* at sites with and without added beehives in the Black Ranges and Toolangi State Forests, Victoria. Four control and four experimental sites were established in these montane forests with each of the experimental sites receiving 6 hives of honeybees. The reproductive performances of the colletid bee was measured in these plots over two seasons. Preliminary analyses suggest that there is no conspicuous impact of honeybees on this bee, though pupal masses maybe slightly, lower at experimental sites (A Spessa pers. comm.). Other explanations for these lower weights, however, still need to be explored.

In each of these studies, the introduction of hives of honeybees is assumed to reduce the availability of floral resources at experimental sites relative to the control sites. None of the studies, however, measured resource abundance at control and experimental sites in sufficient detail to determine if resource availability was reduced following the introduction of hives. This information is needed to properly interpret responses of native bees. If resources declined yet the reproductive outputs of native bees were not affected then honeybees were not competing with native bees. On the other hand, if the availability of floral resources did not change following the introduction of additional hives of honeybees then concluding that no competition exists when the reproductive outputs of native bees at control and experimental sites were the same may be incorrect for two reasons. First, simply introducing hives of honeybees does not guarantee that there will be an increase in honeybee activity at the flowers being used by the native bees being studied at the

Table 10 Composition of established and founder nests of *Exoneura asimillima* at control plots and experimental plots in Nadgee Nature Reserve, NSW in Feb *1987.* Sugden and Pyke *(1991)* removed all the *Xanthorrhoea* scapes from each of eight 10 x 10 m plots at an experimental site and eight similar sized plots at control sites. To each of these plots they added approximately 10 active nests and *44* blank scapes which served as potential nest sites for founder colonies on or before *16* Nov *1986. All* nests were then collected on *15* Feb *1987* and their contents scored. Hives of honeybees were stationed near the experimental plots during the experiment. Initially *29* hives were introduced on *12 Nov 1986;* some died; weak colonies were combined; the *17* active colonies remained when the hives were removed on *28* March *1987* (Sugden and Pyke *1991).* Figures are the average number of eggs, larvae, pre-pupae and adults in nests taken from different sites.

	Founder nests		Established nests	
	Experimental	*Control*	*Experimental*	*Control*
No. of colonies (n)	*47**	*29*	*64*	*64*
No. of adult males	*0.02*	*0.04*	*3.85*	*7.30**
No. of adult females	*1.81*	*1.69*	*6.75*	*10.68**
Large larvae and pre-pupae	*0.89**	*0.21*	*1.46*	*1.03*
Eggs and small larvae	*0.64**	*0.04*	*0.07*	*0.21*
Total	**3.44***	**1.86**	**15.02**	**21.54***

* significantly greater than the equivalent data for control or experimental plots (p<0.05 at least)
  totals as given in Pyke and Sugden (1991), not equal to the sum of eggs, larvae, pre-pupae and adults

experimental sites. Honeybees from hives will spread their foraging effort over a large area; conservatively estimated at 12 km^2 (Visscher and Seeley 1982; Winston 1987). Thus any effect that the additional honeybees may be having on floral resources may be dissipated over a large area and have a relatively small effect on native bees in any one area that is difficult to detect. Furthermore, although control sites may be beyond the normal flight ranges of honeybees stationed at an experimental site, their presence at flowers in other areas may force honeybees from other (feral) colonies to re-distribute their foraging effort such that the amount of foraging done by honeybees in control areas also increases. Second, increases in the numbers of honeybees working flowers does not necessarily mean that honeybees will have a larger share of the resources. Paton (1990) showed that increases in the numbers of honeybees working flowers had a diminishing effect on the proportion of floral resources that they consumed; at relatively high densities of honeybees the addition of further honeybees did not increase their share of the resources. In each of the above studies there were background levels of feral honeybees and these may have already been consuming most of the available resources; introducing additional hives may have had no added effect on the resources available to native bees. In future, measuring the responses of native bees to the removal of feral colonies of honeybees from an extensive area may be a more appropriate manipulation than introducing additional hives of honeybees.

Effects of honeybees on the foraging behaviour and abundance of nectar-feeding birds

In Australia, more than 100 species of birds have been seen harvesting nectar from flowers (Ford *et* al. 1979). Most of these are species of honeyeater (Meliphagidae), some of which depend on nectar or similar carbohydrates for energy (Paton 1980, 1982a, 1988). Numbers of honeyeaters living in areas in southern Australia are often correlated with the quantity of nectar being produced, and breeding usually coincides with periods of abundant nectar (Ford 1979; Ford and Paton 1985; Paton 1979, 1985; Pyke 1983, 1988; Pyke and Recher 1986). In some cases, the birds defend clearly defined feeding territories in which dominant individuals aggressively exclude intruders to gain more or less exclusive use of nectar in their territories (Ford 1981; Paton 1979, 1985, 1986; McFarland 1986c; Newland and Wooller 1986). Although honeyeaters can defend floral resources from subordinates they cannot prevent honeybees from removing a substantial share of the resources (table 7; Paton 1979, 1985). Given the importance of nectar to these birds such losses of nectar to honeybees are likely to affect the abundance and behaviour of the birds.

Only Paton and co-workers (1993, unpubl.) have experimentally manipulated honeybee numbers and measured the responses of birds to these manipulations. Two studies

have been executed. The first involved documenting the behavioural responses of New Holland Honeyeaters, Phylidonyris novaehollandiae to changes in the numbers of honeybees foraging at flowers of Caltistemon rugulosus during spring at Scott Conservation Park, near Goolwa, South Australia. The second involved measuring the numerical responses of honeyeaters to the introduction of commercial loads of honeybees to Banksia *ornata* heathlands during winter in Ngarkat Conservation Park.

In the Callistemon study all of the nectar being produced by the plants was being consumed by floral visitors, predominantly New Holland Honeyeaters and/or honeybees. The numbers of honeybees working the flowers increased: with proximity to a large apiary on the western boundary of the park; seasonally as honeybees switched to Callistemon flowers as other resources declined; and after the introduction of ten additional hives to an experimental plot. Honeyeaters responded to increases in the numbers of honeybees working Callistemon flowers by reducing the frequency with which they visited individual flowers. For example, when few honeybees worked the flowers, New Holland Honeyeaters visited individual flowers on average 9.6 times/day, but when honeybee activity was high this visitation was reduced significantly to only 3.0 visits/flower/day (Paton 1993; table 11). In addition the birds adjusted their foraging by avoiding the flowers that were most extensively used by nectar-feeding honeybees.'

Honeybees showed distinct preferences for certain flowers when harvesting nectar from this Callistemon. For example, they visited flowers at the two ends of an inflorescence more frequently than those in the centre (table 12). They also favoured inflorescences exposed on the ends of branches at the periphery of the plant's canopy over those that were completely or partially hidden by foliage within the plant (table 12). These patterns of use by honeybees are easily explained by the ease with which different flowers can be visited by honeybees (see Paton 1993 for details).

New Holland Honeyeaters responded to these patterns. In the absence of honeybees, New Holland Honeyeaters showed no patterns to floral visitation, visiting all flowers equally (table 13). However, when honeybees were working the flowers, the birds showed a strong bias to inflorescences borne deep within the canopy of a plant and also a strong bias to visit the centrally-located flowers within an inflorescence (table 13). On average these inflorescences and flowers had higher standing crops of nectar than the flowers and inflorescences being used extensively by honeybees (Paton unpubl. data). Clearly, honeybees altered the foraging patterns of the birds, with the birds concentrating their foraging activity at the flowers used least by honeybees. The presence of honeybees working the flowers may also influence diurnal patterns of foraging by honeyeaters. When honeybees were present in only small numbers, New Holland Honeyeaters foraged more or less equally throughout the day. However, when

Table 1 1 Changes in the frequency with which New Holland Honeyeaters visited the flowers of *Callistemon rugulosus* and changes in territory sizes for these birds with changes in the numbers of honeybees working the flowers near Goolwa, SA in spring *1983.* Honeybee activity was scored by counting honeybees at *50-200* inflorescences at regular intervals through the day and converting these to bees per 1000 flowers. Daily visitation by birds involved counting the number of visits made by birds to samples of flowers during five 1 hour periods spread evenly over a *14* h day. Data are expressed as mean ± se (n), where n for honeyeater visits is the number of independent determinations made during the level of honeybee activity, and n for territories is the number of territories measured. Visitation rates by birds to flowers were significantly lower (ANOVA, F = *12.7,* df = *3,32, p<* *0.001),* and territory sizes significantly larger (ANOVA, F = *21.3,* df = *3,106, p<0.001*) when honeybee numbers were higher.

Maximum no. of honeybees seen per 1000 flowers	Honeyeater visits/ flower/day	No. of flowers in honeyeater territories
0.0-5.0	*9.6+ 0.8(9)*	*4343 + 185 (16)*
5.1-10.0	*5.5+ 1.0(9)*	*5387+ 219(38)*
10.1-15.0	*5.0 ± 0.8(9)*	*61 12 + 306(28)*
> 15.0	*3.0+ 0.3(9)*	*7606+ 304(28)*

honeybees were frequent visitors to flowers, honeyeaters foraged more intensively early in the morning and less so during the middle of the day when honeybees were most active (Figure 1). Thus losses of nectar to honeybees during the middle of the day may also affect diurnal patterns of foraging in the birds. Bond and Brown (1979) showed similar diurnal patterns of activity for honeyeaters and honeybees foraging on E. incrassata nectar, as did Paton (1979,1985) for New Holland Honeyeaters and honeybees visiting a range of other plant species. Stace (1988) subsequently concluded that this habit of birds foraging intensively early in the morning, with honeybees foraging in the middle of the day, eliminated much of the potential competition between honeyeaters and honeybees. However, Stace (1988) did not consider the possibility that foraging by honeybees in the middle of the day influenced when the birds foraged. Another assumption was that honeyeaters could harvest much of their daily food requirements during the first few hours of the day and store this food for later use. Initial research, however, shows that honeyeaters may have a limited capacity to rapidly store energy, and when given the opportunity prefer to steadily accumulate food reserves throughout the day (eg Collins and Clow 1978; Collins and Morellini 1979; Collins et at. 1980). In any case a moderate

Table 12 Spatial patterns in the use of *Callistemon rugulosus* flowers by nectar-collecting honeybees. Use of inflorescences on a plant was scored by counting the numbers of honeybees foraging at 250 inflorescences fully exposed on the exterior of the plant's canopy, 250 partially covered and 250 fully covered by the plant's foliage. Use of flowers on an inflorescence was scored by dividing the inflorescence into three equal parts (proximal, middle and distal third) and counting the numbers of honeybees foraging at flowers in each third. Honeybees used exposed inflorescences more extensively than those that were partially or fully covered (X^2 = 26.4, df = 2, p<0.001) and used flowers in the distal and proximal thirds of an inflorescence more than flowers centrally located within an inflorescence (X^2 = 25.8, df = 2, p<0.001).

Position of inflorescence *on plant*	*No. of* honeybees *counted*	Position of flower on inflorescence	*No. of honeybees* counted
exposed	95	proximal third	248
partially covered .	61	middle third	191
fully covered	37	distal third	394

Table 13 Spatial patterns to the use of *Callistemon rugulosus* flowers by New Holland Honeyeaters in the presence and absence of honeybees. Use of inflorescences was scored by recording the frequency with which honeyeaters visited inflorescences that were exposed, partially covered or fully covered by the plant's canopy during one hour observations. Exposed inflorescences were more numerous than partially covered and fully covered inflorescences, so data are expressed as visits per inflorescence per hour to allow easier comparisons. The number of inflorescence hours are given in parentheses. Use of flowers within an inflorescence was scored by recording the numbers of probes made by New Holland Honeyeaters at flowers in the proximal, middle and distal thirds of inflorescences. 550 probes were scored at times when honeybees were not foraging and 1346 probes were scored when honeybees were foraging. New Holland Honeyeaters used all inflorescences and all flowers equally when honeybees were absent (X^2 = 2.59 and 3.00 respectively, df = 2, p>0.05) but favoured covered inflorescences and centrally-located flowers within an inflorescence when honeybees were present (X^2 = 727 and 133 respectively, df = 2, p<0.001).

| Position *of flower or inflorescence*	*Frequency of use by New Holland Honeyeaters*	
	Honeybees absent	*Honeybees present*
Inflorescences	**visits/inflor/h**	**visits/inflor/h**
exposed	3.44 (133)	1.26 (848)
partially covered	3.68 (57)	2.62 (424)
fully covered	3.00(29)	4.06 (193)
Flowers	**% of 550 probes**	**% of 1346 probes**
proximal third	34.2	28.2
middle third	35.8	47.9
distal third	30.0	23.9

level of foraging continues throughout the day even in the presence of honeybees (Paton 1979, 1982a, 1985; Bond and Brown 1979; Figure 1).

These responses of honeyeaters to losses of food to honeybees are consistent with a competitive interaction but they are not sufficient on their own to indicate that honeybees were causing population densities of honeyeaters to decline. Paton (1993), however, also examined the effect of nectar losses to honeybees on the sizes of the territories being defended by New Holland Honeyeaters **using** C. rugulosus. If honeybees have no influence on the ability of the birds to harvest nectar, then changes in the numbers of honeyeaters working flowers should not alter the sizes of the birds' territories. However, the number of Callistemon flowers defended by territorial New Holland Honeyeaters increased significantly when the numbers of honeybees working the flowers increased (table 11). When large numbers of honeybees were visiting the flowers, New Holland Honeyeaters defended more than 7000 flowers, almost double the number being defended when only a few honeybees were working the flowers (table 11). This doubling of territory size was consistent with the amounts of nectar (ca

50% of production) calculated to be lost when large numbers of honeybees were foraging (ie > 15 honeybees/ 1000 flowers) at Callistemon flowers.

This increase in territory size with increases in honeybee activity was also supported with some experimental evidence (Paton 1993). When the number of honeybees working flowers was increased experimentally by placing 10 hives next to a patch of Callistemon, the dominant birds (adult males) in that patch expanded their territories by displacing subordinates (juveniles and females) from adjacent territories and adding all or parts of these territories to their own. In the experimental patch the territories of five dominant birds increased significantly from 4744 ± 216 (se) to 7523 ± 290 (se) flowers after the introduction of the bee hives (ANOVA, $p < 0.001$, Paton 1993; table 14). This increase in territory size was consistent with. changes of from around 10% to approximately 50% of food lost to honeybees following the. introduction of the beehives. In control areas where honeybee numbers did not change, territories of five individual birds did not increase significantly (table 14). Note, however, that the responses of individual birds within a patch are not strictly independent.

Figure 1 Diurnal changes in the percentage time spent foraging by individual New Holland Honeyeaters when the numbers of bees working C. rugulosus flowers were low (dashed lines) and when they were high (solid lines). Each point is the percentage time of a 1 hour time budget spent foraging. Data collected Oct-De, 1983 at Scott CP, SA.
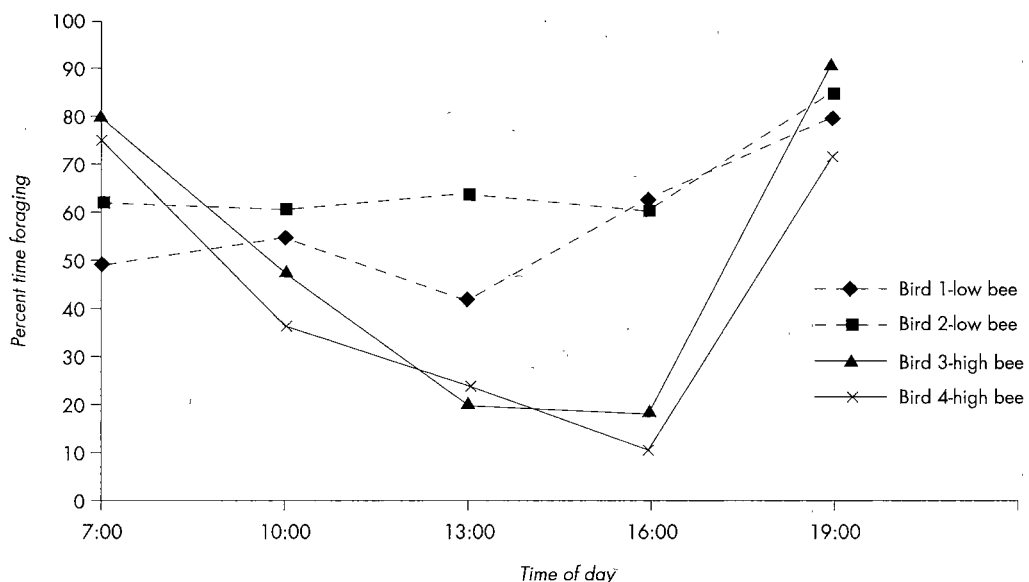
Although this manipulation of honeybee numbers and subsequent territorial responses of honeyeaters needs to be replicated, the results of this trial are consistent with the other behavioural responses that were recorded following changes in honeybee activity at *Callistemon* flowers. The results suggest that the numbers of honeyeaters living in an area could be reduced to about a half of the carrying capacity expected if honeybees were absent. Furthermore, females appear to be displaced more frequently than males and this disproportionate loss of females may affect honeyeater population dynamics more than if both sexes were displaced equally (Paton 1993) .

Paton (1979, 1985) also showed that territorial New Holland Honeyeaters held larger feeding territories on a range of other plants when honeybees were also harvesting the floral resources from these plants. Again the increase in the size of the territories (numbers of flowers defended) matched the amounts being consumed by honeybees such that the birds still defended sufficient resources to meet their energy requirements.

These results are consistent with honeybees competitively excluding some birds from flowers but they contrast dramatically with studies on changes in the numbers of honeyeaters using *Banksia ornata* heathlands during winter in Ngarkat CP following the introduction of beehives.

Ngarkat CP is an important overwintering site for commercially-managed honeybees in South Australia. In all there are over 200 registered apiary sites within this reserve, though typically only about 80 sites are stocked with honeybees in any one year. Most of these sites are in the western and southern sections of the reserve with beekeepers shifting hives into the area in late May and maintaining them in the reserve until late July or early August. The primary plant species providing floral resources during this period is the desert banksia, *Banksia ornata* and in most years native animals are unable to prevent floral resources (both nectar and pollen) from accumulating at these inflorescences (Paton *et at.* unpubl.).

Table 14 Changes in the sizes of territories of New Holland Honeyeaters following the introduction of 10 hives of honeybees to an experimental site. Upon the introduction of the hives the frequency with which honeybees visited *C. rugulosus* flowers increased from 0-8 visits/flower/day to 36-44 visits/flower/day. On the control sites visitation rates also increased but not to the same extent; from 0-5 visits/flower/day to 16-21 visits/flower/day. These changes in honeybee numbers resulted in food losses increasing from 0-10% to 40-50% after the extra hives arrived at the experimental site. At the control site losses to honeybees increased from 0-10% to 20-25%. Individually colour-banded honeyeaters were watched for up to 5 h to determine the boundaries of their territories. The numbers of inflorescences present in each territory was then counted and the numbers of flowers calculated by multiplying the number of inflorescences by the mean number of flowers counted on 50 inflorescences selected within each of the territories.

Treatment	Bird#	Territory size (no. of flowers)	
		before honeybees	after honeybees
Experimental site	1	5132	7426
	2	4556	7930
	3	4368	8060
	4	5376	7754
	5	4290	6445
	mean	4744	7523
	se	216	290
Control sites	6	3167	4587
	7	4004	4739
	8	4554	4374
	9	3454	3736
	10	3690	3858
	mean	3774	4259
	se	239	198

Since 1990; Paton and co-workers have been assessing the impact of commercial beekeeping operations on the flora and fauna of Ngarkat CP to help land managers decide whether to allow continued use of the reserve by beekeepers. The research involved selecting 15 sites (each at least 3 km away from any other site) within the central part of the reserve. Most of this area had had no previous history of commercially-managed honeybees and densities of feral colonies were negligible (0.001 col/ha). Some of the sites and not others then received commercial loads of honeybees in one or more seasons and the responses of native biota to those manipulations measured. Amongst the taxa considered were nectar-feeding birds, small mammals, native bees and several other groups of flower-visiting insects, including ants and staphylinid beetles. The research also involved measuring the production and availability of floral resources and seed production by the plants.

Although the presence of honeybees reduced the quantities of nectar available at *Banksia* inflorescences, particularly near apiaries, there were still considerable quantities of nectar remaining at the end of the day when honeybee foraging had ceased (table 15; Paton *et at.* MS3; unpubl.). The quantities of nectar left over often exceeded 0.5 g of sugar/inflorescence even within 100 m of an apiary. These leftover quantities were still more than adequate to satisfy native fauna. For example, a typical 20 g honeyeater needs about 5 g of sugar per day to satisfy its energy requirements (eg Paton 1982a). So even within 100 m of an apiary the bird still only needed to visit 10 inflorescences at the end of the day to collect its daily energy requirements. In these areas there can be 1000 inflorescences in bloom/hectare so even after the birds and bees had fed during the day there was still enough food left over to feed the equivalent of another 100 birds/ha.

Consistent with this surfeit of food there were no significant differences in the numbers of honeyeaters counted at sites stocked and not stocked with honeybees (table 16). Nor were there any significant differences between sites with and without honeybees in the numbers of small nectar-feeding mammals caught in pitfalls or invertebrates counted at inflorescences (Paton *et at.* MS3).

So surplus floral resources existed in this system and although honeybees depressed food availability, the level of depression was not sufficient to affect the abundance of native fauna in these heathlands. One explanation for the existence of surpluses is that there were insufficient native fauna, particularly birds, at Ngarkat to fully exploit floral resources. In other *B. ornata* healthlands closer to the coasts of South Australia, densities of honeyeaters ranged from 6-22.5 honeyeaters/ha when *B. ornata* was flowering, two to eight times the density recorded at Ngarkat (Paton unpubl.). Honeybees were also prominent at inflorescences in these areas. One reason why there might be relatively few birds in Ngarkat during winter when *B. ornata* flowers is because this area produces few suitable flowers for these birds during summer and autumn and so many of the birds must leave the park for that period. The areas that will produce suitable resources for these birds during summer and autumn are the more mesic coastal and woodland areas. These areas, however, have been extensively and disproportionately cleared for agriculture compared to the drier sandy areas like Ngarkat that are least suited to agriculture. As a result, population- sizes of honeyeaters in the region as a whole may be severely limited by the availability of nectar sources during the summer and autumn months. Thus honeyeaters cannot recruit back into the drier heathland habitats of Ngarkat in sufficient numbers to fully exploit floral resources during winter. Such an explanation is consistent with seasonal patterns to nectar availability that have been reported from other areas in general (see above) where summer sources are more heavily exploited than winter sources in many areas. Furthermore, honeybees usually consume a larger share of the floral resources being produced during the warmer months of the year and may depress resources further for honeyeaters at these times. The irony of this scenario is that experiments to measure the impact of honeybees on the flora and fauna of Ngarkat CP should probably have involved manipulating honeybee numbers in areas outside the park and at other times in the year rather than manipulating the numbers of honeybees using this reserve in winter when *B. ornata* was flowering.

Table 15 Quantities of nectar remaining at *Banksia ornata* inflorescences in late afternoon at sites stocked and not stocked with honeybees in Ngarkat CP during the winter of 1990. Inflorescences were collected at approximately 1600h, after honeybee activity had ceased for the day. This was accomplished by carefully placing a plastic bag over the inflorescence and snapping off the inflorescence so that any dislodged nectar would be collected in the bag. Nectar was removed using the centrifuging technique of Armstrong and Paton (1990) and the volume and concentration measured and used to calculate the grams of sugar present in the nectar. Nine sites were sampled in each month (3 stocked with honeybees and 6 without honeybees). For these monthly samples 12 inflorescences were collected at 100 m and 12 inflorescences at 1000 m from the central point of each site; 6 inflorescences being collected at each distance along each of the two transects established for bird censusing (see table 16). The mean quantity of sugar per inflorescence ± se is given in the table, where n is the number of inflorescences sampled. Almost identical patterns were found in 1992 and 1993 (not shown). No bees were placed in the park in 1991. Although the quantities of nectar remaining at inflorescences near apiaries is lower than control sites and lower than for inflorescences 1 km from the apiary, there are still substantial quantities of nectar left unexploited by honeybees near apiaries.

Month	sugar (g) per inflorescence	
	sites with honeybees	sites *without honeybees*
	100 m from the central point of each site	
June	1.15 ± 0.04 (36)	1.52 ± 0.07 (72)
July	0.59 ± 0.20 (36)	1.35 ± 0.39 (72)
August	0.49 +0.14(36)	*0.70+0.14* (72)
	1000 m from the central point of each site	
June	1.40 +0.26(36)	1.62+0.02 (72)
July	1.22 + 0.32 (36)	1.10 + *0.27* *(72)*
August	0.86 + 0.05 (36)	0.66 ± 0.17 (72)

Table 16 Densities of honeyeaters (no./ha) at sites stocked and not stocked with commercial loads of honeybees in Ngarkat CP, SA. Honeyeaters were counted along two 1500 m transects radiating out from the central point of each of the 15 sites. Each transect was marked with flagging tape, at 50 m and 100 m intervals. Observers walked these transects at the rate of 4 minutes/100 m commencing at 8 am. All birds seen within 50 m of the transect line were recorded for each 100 m section of the transect. Birds that flew over were also noted. Birds along each transect were counted twice during a census, once on the way out and again on the way in. In the following table, densities of honeyeaters are shown for the first 500 m of transects (from the central point). Data from separate sites have been pooled for ease of presentation. In 1990 and 1992 five of the fifteen sites were stocked with honeybees while in 1993 nine sites received commercial loads of honeybees. No honeybees were placed on sites in 1991 because of a drought. The table shows the mean ± se number of honeyeaters counted per hectare for sites with and without commercial loads of honeybees. Samples sizes are the number of independent censuses made at the two types of sites. Densities of honeyeaters were not significantly lower at sites stocked with honeybees.

Year	Number of honeyeaters per hectare	
	sites *without* honeybees	sites *with honeybees*
1990	2.89 + 0.39 (46)	2.92 + 0.29 (20)
1992	2.26 ± 0.16 (60)	2.21 ± 0.24 (30)
1993	2.29 ± 0.17 (36)	2.61 ± 0.16 (54)

Effects of honeybees on the pollination of Australian plants

Honeybees could alter the pollination rates of Australian plants in many ways. They could:

1. add to the pollination services provided by native fauna leading to increases in seed production;
2. displace native pollinators from flowers without providing equivalent pollination services leading to declines in seed production;
3. alter the behaviour of native pollinators in ways that alter patterns of pollen dispersal leading to changes in seed production; and
4. remove pollen from flowers reducing the quantities of pollen being transferred to flowers by legitimate pollinators again reducing seed production.

These potential impacts of honeybees on native flora have rarely been considered in Australia.

Matthews (1984) raised two issues concerning interactions between honeybees and native flora: that honeybees were inefficient pollinators of some native plants; and that honeybees may increase rates of hybridisation between plant species. Evidence that hybridisation between coflowering plant species has been facilitated by honeybees, however, is lacking. In fact, many species of native fauna are just as likely to effect interspecific pollen flow as honeybees, if not more so, judging from the mixed pollen loads collected from many native birds, mammals and insects (Paton and Ford 1977; Hopper 1980b; Ford and Paton 1982; Ford and Pursey 1982; Bernhardt *et al.* 1984; Kenrick *et al.* 1987). Honeyeaters also frequently switch from feeding at the flowers of one plant species to another when two or more suitable species are flowering nearby and will defend territories that include more than one species of flowering plant (Paton 1979, unpubl.; Hopper and Burbidge 1986). Under these conditions honeyeaters are likely to effect interspecific pollen flow. Gross (1992) also reports that native bees *(Trichocoltetes sp)* frequently shifted from one species of pea to another species of pea during foraging bouts if two or more similar species of pea were interspersed. Despite the

frequency of interspecific movements by pollinators, the frequency of hybrids is low, suggesting that post-pollination mechanisms in the plants effectively select against interspecific pollen. Even if hybrids were prominent, separating the contribution of honeybees from that of native fauna in the production of these hybrids would be difficult. Moreover, Wapshere (1988) also indicated that the rate of hybridisation amongst *Phebalium,* a genus of Australian insect pollinated plants, was no greater than the rate of hybridisation amongst *Casuarina,* a genus of Australian plants usually pollinated by wind.

Most of the concern about honeybees affecting native flora, however, is based on observations that honeybees forage at flowers of some native plants in ways that differ from native pollinators and in ways that were less likely to effect pollination. For example, honeybees rarely touched the stigmatic and pollen-bearing surfaces of several predominantly vertebrate-pollinated taxa including *Grevillea, Banksia, Amyema* and *Callistemon* when harvesting nectar, though pollen-harvesting honeybees visiting these plants made more frequent contact with stigmatic surfaces (Paton and Turner 1985; Paton 1986, 1993, unpubl.; Taylor and Whelan 1988; Vaughton 1992). Bell (1987) also suggested that honeybees robbed nectar or visited the flowers of *Templetonia retusa,* and species of *Crotalaria, Erythrina, Bossiaea, Gastrolobium, Oxylobium, Calothamnus, Banksia* and *Beaufortia* in ways that bypassed the stamens and stigma but provided no quantitative data. Other examples, include Gross's (1993) observations of honeybees contacting the stigmas of the bee-pollinated <u>*Melastome*</u> *affine* less frequently than most of the native bees that visited the flowers. Honeybees also differed from many of the native bees by not buzzing the anthers of this plant to collect pollen. Instead they occasionally harvested pollen that had previously been deposited on stigmas. Although these examples suggest some inefficiency on the part of honeybees, honeybees can still effect some pollination at many of these plants. For example, Vaughton (1992) showed that inflorescences of *Banksia spinulosa* that were caged to exclude birds but not honeybees set comparable quantities of seed to open-pollinated flowers where both birds and bees had access, but only late in the season when honeybees were frequent

visitors to flowers. Similarly caging experiments showed that honeybees were capable of pollinating Banksia ericifolia, *B.* ornata, Callistemon *rugulosus* and *Correa reflexa* although the quantities of seed produced may be lower than that effected when birds also had access (Paton and Turner 1985; Paton 1993 and see below). Any ineffectiveness in the pollinating abilities of honeybees, however, is unlikely to have a significant negative effect on seed production unless honeybees have displaced a substantial number of native pollinators from the plants or altered the quantities of pollen available for dispersal by native animals.

Paton (1993) considered the impact of honeybees on seed production by Callistemon rugulosus in a small reserve near Goolwa, South Australia. This Callistemon was largely self-incompatible and needed crosspollination to set substantial quantities of fruit. When 685 flowers were cross-pollinated by hand 45.4% set fruit, but only 11.0% of 610 bagged flowers set fruit following selfpollination. Thus to be effective, pollinators should regularly contact the reproductive parts of the flowers and move frequently between plants. Honeybees harvesting nectar from Callistemon, however, only struck the stigma on 4.4% of visits (in over 8000 observations). Pollen-harvesting honeybees struck the stigma more frequently but still on only 16.7% of 1649 visits scored. New Holland Honeyeaters, on the other hand, frequently contacted the stigma of the flower being probed (>50% of occasions) as well as adjacent flowers (determined from photography). Honeybees also rarely moved between plants. For example, in areas where individual plants were widely spaced (>3 m apart) individual honeybees were tracked for a total of 9.9 hours and were observed probing over 4600 flowers.' Not once during these observations was a honeybee observed to fly to an adjacent plant. In these areas territorial New Holland Honeyeaters moved between plants 7.3 times per hour (10 hours of observation), equivalent to one interplant move every 400 probes. Thus when honeybees displace honeyeaters from patches of Callistemon (see tables 11, 14), the quality of the pollination service should decline. If seed production is limited by pollinators then such a displacement of a more effective pollinator by a less effective one should lead to reduced seed production and such a pattern was found.

Rates of fruit production for C. rugulosus varied with the numbers of bees and birds working the flowers. First, the numbers of flowers that set fruit inside wire mesh cages, which excluded birds, increased as the numbers of bees increased (table 17) indicating that honeybees could pollinate Callistemon flowers. However, the rates at which caged flowers set fruit (7-17%; table 17) were similar to rates achieved following self-pollination (11%) and well below those achieved after cross-pollination (45%). The low fruit production at caged flowers was therefore consistent with honeybees effecting little cross-pollination for this population of Callistemon. Fruit production at flowers exposed to both birds and bees, however, was significantly higher than that for caged flowers (table 17), indicating that birds provided important pollination services to the plant. Furthermore, this fruit production declined significantly from 35.1% to 22.6% as the numbers of honeybees using the flowers increased (table 17). Thus displacement of pollinating birds by less effective honeybees reduced fruit production for this population of Callistemon. Honeybees may also alter rates of pollination for *Correa reflexa* by removing pollen that would otherwise be dispersed by birds (Paton 1993). Honeybees mainly visited recently-opened flowers of C. *reflexa for* pollen and rarely visited older flowers. Recently-opened flowers were in male phase and rich in pollen while older flowers were in female phase. Because they preferred male flowers, honeybees only pollinated the occasional *Correa* flower and were not as effective as birds which visited all floral stages. When both birds and honeybees had access to the flowers, 26. 1% of flowers produced fruit. However, when birds but not honeybees were excluded from flowers fruit production dropped significantly to 10.7% (Paton 1993). Thus honeybees were not as effective as honeyeaters in pollinating this plant.

Visits to flowers by honeybees often outnumbered those by birds (eg table 6; Paton unpubl.) and honeybees were often the first to visit recently-opened flowers, dislodging 87% of the pollen on their first visit (Paton 1993). In comparison, several species of honeyeater only dislodged an average of 34-53% of the pollen on their first visit to a virgin flower (Paton 1991, unpubl.). On many occasions recently-opened flowers

were visited several times by honeybees so little pollen remained when the flower was first visited by a bird. At times honeybees even chewed undehisced anthers to rob pollen from flowers that were just opening. Paton (1993) measured the impact of this pollen loss on subsequent pollination by birds with a series of simple aviary trials. Captive Eastern Spinebills, *Acanthorhynchus tenuirostris* were presented with eleven *C. reflexa* flowers: a source flower that supplied pollen and ten sink flowers that received pollen. Sink flowers had been emasculated before the anthers dehisced and so contained no pollen. Thus any pollen that these flowers received during trials must have come from the source flower. The ratio of source flowers to sink flowers in these trials approximates the natural ratio. The flowers of C. *reflexa* live for about nine days. Consequently one flower in nine would be expected to have released pollen in the last 24 hours. In each trial, captive honeyeaters were allowed to visit each of the flowers between five and ten times (table 18), similar to the frequency with which birds visited *Correa* flowers in the field (eg table 6). All flowers were then retrieved and the pollen deposited on the stigma of each flower counted under a microscope. The amount of pollen initially present at the source flower was then varied and any differences in pollen receipt by the sink flowers measured. To vary the amount of pollen at source flowers and mimic pollen loss due to bee visits, up to seven of the eight anthers were removed. When pollen was removed from source flowers, significantly fewer sink flowers

received pollen (table 18) and the total number of pollen grains landing on their stigmas was also significantly reduced (table 18). Appropriate field work is now required to determine if this also happens in the field and leads to reduced production of seeds for this plant in areas stocked with honeybees, but the data indicate the potential for honeybees to have a negative effect on pollination rates for this bird-pollinated plant.

Pyke (1990) reports a similar finding for Christmas Bells, *Blandfordia nobilis* flowering in Barren Ground Nature Reserve near Jamberoo, NSW. In some years, honeybees apparently removed so much pollen that the effectiveness of pollen transfer by honeyeaters, the native pollinators, was reduced and seed production consequently reduced but Pyke (1990) provided no quantitative data.

These studies showing the negative effects of honeybees on the seed production of plants need to be balanced against other studies where honeybees have been found to aid rates of pollination.

In Ngarkat CP seed production by *B. ornata* was significantly enhanced at sites stocked with honeybees in each of three years (table 19). At sites without honeybees seed production ranged from 4-7 seeds per inflorescence, while at sites with honeybees seed production ranged from 8-11 seeds per inflorescence. There were also differences between years in overall seed production but in all years seed production was significantly increased in the presence of honeybees.

Table 17 Fruit production by flowers of *Callistemon rugulosus* placed inside and outside wire mesh cages at three levels of honeybee activity: low (ca 5 bees/1000 flowers daily maximum); medium (ca 10 bees/] 000 flowers); and high (ca 15 bees/1000 flowers). The wire mesh cages excluded birds but did not alter visitation rates to flowers by honeybees. Note that when honeybee activity is high bird activity is low (table 11). Data were collected from 12 plants with each plant having a caged and uncaged treatment, and then pooled. Total number of flowers in each treatment are given in parentheses. Although there was significant heterogeneity between replicates, that heterogeneity results in analyses of pooled data being, if anything, conservative. Analyses of pooled data show: that fruit production increased significantly for caged flowers as honeybee activity increased (X^2 = 45.1, df = 2, p<0.001); that fruit production at caged flowers was significantly lower than at uncaged flowers (X^2 = 181.6, 121.6, and 12.8 for low, medium and high densities of honeybees respectively df = 1, p<0.001); and that uncaged flowers exposed to birds .and bees declined significantly with increases in honeybee activity (X^2 = 38.0, df = 2, p<0.001).

Level of honeybee activity	% flowers setting fruit inside wire cages (honeybees *only*)		% flowers setting fruit outside wire cages (honeybees *& birds*)	
low	6.7	(735)	35.1	(770)
medium	15.3	(2584)	27.9	(2662)
high	17.1	(1317)	22.6	(1330)

Although these figures show that honeybees enhanced the seed production of *B. ornata* they do not and cannot be used to infer that honeybees were better pollinators than native fauna. The primary reason for the poor performance by *B. ornata* in Ngarkat CP was insufficient native fauna, not ineffective pollination by those that were present.

In this reserve native pollinators were unable to fully exploit all of the floral resources being produced *by B.* ornata (see above) and unable to pollinate sufficient flowers to maximise seed production. At sites not stocked with honeybees, seed production was easily enhanced following additional cross-pollination, indicating that native pollinators were insufficient. At sites stocked with

Table 18 Influence of pollen availability at source flowers on subsequent dispersal of pollen to sink flowers by captive Eastern Spinebills visiting *Correa reflexa* flowers. Differences in the number of sink flowers receiving pollen and in the number of pollen grains deposited were significant (ANOVA, F = *7.9,* df = *2,37, p <0.001* in both cases). Note that source flowers with 1 intact anther (instead of *8)* have had *87%* of their pollen removed, which is the average quantity removed by honeybees on their first visit to a flower. This treatment mimics the removal of pollen by honeybees in the field (see table *7)* where honeybees account for up to *93%* of the pollen produced by the plant at times. With *87%* of the pollen removed only *25%* of the sink flowers are pollinated by Eastern Spinebills and those flowers only receive an average of *5.8* pollen grains each. More flowers are pollinated and the quantities of pollen deposited are significantly higher when pollen is available. Values given are means + se.

Intact anthers on source	No. of trials	No. of probes into sink flowers	No. of sink flowers receiving pollen	Total no. of grains deposited on the ten sink flowers
8	15	7.3±1.0	6.2±0.7	89.6±14.0
4	12	7.9 ± 1.0	5.4+0.7	51.8 ± 19.1
1	13	6.9+0.7	2.5+0.7	14.6+,4.5

Table 19. Seed production for *Banksia ornata* at sites stocked and not stocked with honeybees at Ngarkat CP in three separate years. Seed production was consistently and significantly higher at sites stocked with honeybees in each of the three years. At sites not stocked with honeybees seed production was enhanced significantly following additional cross-pollination by hand, but was not at sites that were stocked with honeybees. In *1990* inflorescences only received a single supplementary pollination but in subsequent years each inflorescence was given supplementary cross-pollination at least twice. This accounts for the lower seed production following additional pollination in *1990,* since on any one day only a percentage of the flowers on an inflorescence would be receptive, and so fewer flowers received additional cross-pollination in that year. Data show the mean ± se (number of follicles (equivalent to seeds) produced/ inflorescence). For convenience in presentation, data from replicate sites in each year have been pooled. In *1990* and *1992* five of fifteen sites were stocked with commercial loads of honeybees *(40-100* hives), while in *1993* nine sites received honeybees. Sample sizes in *1990* were reduced because 1 1 of the *15* sites were burnt in a wildfire before follicle production could be scored. Drought conditions prevented hives from being placed on any sites in *1991.* The table only includes data collected on inflorescences close to the central point of each site since this was where the greatest reduction of floral resources (by honeybees) took place.

Year	Number of follicles produced per inflorescence	
	natural rates	rates following additional cross pollination
Sites without honeybees		
1990	3.76±0.26(181)	6.08±0.37(91)*
1992	5.43 ± 0.54 (500)	9.21 ± 0.58 (500)*
1993	7.32 ± 0.64 (225)	11.47 ± 0.24 (225)*
Sites with honeybees		
1990	11.30 + 0.60 (127)**	10.62±0.69(71)
1992	8.30 + 1.04 (250)**	9.81 ± 0.87 (250)
1993	10.92 ± 0.54 (252)	12.27 ± 0.59 (249)

* significant increase in seed production following additional cross pollination (p<0.001) **

significantly higher seed production at sites stocked with honeybees (p<0.001)

honeybees additional cross-pollination of flowers failed to enhance seed production any further (table 19). Thus honeybees were contributing significantly to the production of seeds by this plant and their activity at flowers was sufficient to guarantee that a full complement of seeds was produced.

Although these data indicate that B. ornata benefits from the presence of honeybees in Ngarkat CP, increased seed production may lead to B. ornata becoming more prominent in those heathland communities in future generations, to the detriment of other plants. Enhanced seed production has also been reported for a few species of eucalypts following the introduction of beehives into areas (Loneragan 1979; Moncur and Kleinschmidt 1992; Moncur et al. 1993; Moncur pers. comm.). In most cases this enhancement occurred in stands of eucalypts where natural rates of pollination were low, including eucalypt seed orchards and occasionally natural stands (Moncur and Kleinschmidt 1992, Moncur et al. 1993; Moncur pers.comm.). In each of these studies seed production was measured only as the number of viable seeds produced per capsule and no data were given on the numbers of flowers that succeeded in setting capsules. Furthermore all the studies lacked replication and did not control for possible locational and seasonal effects on seed production. Conclusions that honeybees have enhanced the seed production for these eucalypts, therefore, may be premature.

Comparisons with overseas research on competitive interactions between honeybees and native flowervisiting fauna and flora

Honeybees have also been introduced to the American continent where both descriptive and experimental studies have investigated the effects that honeybees (particularly Africanized honeybees) may be having on native bees. These studies not only provide further examples of potential interactions between introduced honeybees and native fauna, but they also highlight the complexity of the interactions and the difficulty in assessing impacts. Most of the experimental work has been conducted by David Roubik in

Central America, but several North American and German studies have also been conducted.

Schaffer et al. (1979) recorded ari inverse relationship between the numbers of honeybees and other native bees *(Bombus, Xylocopa)* working patches of flowering Agave schottii in Arizona, with honeybees predominating in the most productive patches. There was also some temporal separation in the activities of these bees, with honeybees being more active during the first few hours of the day when standing crops of nectar were highest. Schaffer *et* al. (1979) suggested that this reduced the quantities of nectar available for other animals and hence the use of *Agave* schottii by native bees. Ginsberg (1983) studying the foraging of Apis honeybees and native bees on a variety of wildflowers near Ithaca, New York found a similar pattern with honeybees dominating the richer sources and native bees being more prominent at poorer sources. Schaffer et al. (1983) subsequently manipulated the availability of nectar at stalks of *Agave* schottii by excluding ants. Ants foraged on nectar both during the day and overnight, and consumed a substantial share of nocturnal nectar production. In the first manipulation, ants were excluded with tanglefoot from 10 of about 130 flower stalks in a 1 ha area. These stalks were then visited by greater numbers of both honeybees and bumblebees, *Bombus* compared to control stalks where ants still had access. Ants were then excluded from all of the stalks in and around the study area. Following this manipulation the numbers of honeybees increased again, as did the numbers of small solitary bees but the numbers of Bombus did not increase.

During these experiments, two hives of Cordovan honeybees were present at the site. The subsequent introduction of two more hives had no discernible effect on the numbers of honeybees working the flowers. These hives were then removed and for a short period (3-5 days) the numbers of honeybees working *Agave* schottii were low. Over the next 3-5 days the numbers of *Bombus,* small solitary bees and feral honeybees (distinguished from hive bees by colour) all increased, but once feral honeybee densities reached those present before the hives were removed, the numbers of bumblebees and small solitary bees declined.

Three important findings come from this work.

1. Manipulations of honeybee numbers by shifting small numbers of hives into and out of areas may not lead to any significant change in the numbers of honeybees working the flowers within study plots.

2. The behavioural responses of native fauna may vary depending on the scale of the manipulations. At one scale a behavioural response for *Bombus* was detected but not for smaller solitary bees while at a larger scale no response was detected for *Bombus* (following one of the manipulations) but was detected for smaller solitary bees. Thus in designing field experiments to test the impact of honeybees on native fauna the scale and direction of the manipulations must be carefully considered.

3. Competition for floral resources may still exist even when competing taxa forage at different times of the day and in this case the consumption of nectar by ants, particularly overnight, reduced the amounts available for bees during the day and the use of Agave patches by bees.

Roubik's work in Panama and French Guiana has carried these experimental studies much further. He considers not only behavioural responses of stingless social bees to manipulations of honeybee densities and food resources but also measures the effects of introductions of honeybees on colony performance of these native stingless bees and longer term changes in the abundances of native bees in general. Most of the experimental manipulations were conducted before 1983 in areas where feral Africanized honeybees were either absent or scarce. The manipulations involved exposing native bees to 5-22 hives of honeybees for short periods of time, ranging from 1-30 consecutive days. These experimental studies have shown that honeybees non-aggressively displaced some native social bees from flowers and artificial feeders and that colonies of honeybees were superior to native social bees in their ability to locate and harvest rich floral resources and to respond to changes in the availability of floral resources (Roubik 1978, 1980, 1981, 1982a). Despite being displaced from some floral resources there were no detectable changes in the amount of food stored or brood produced by colonies of native bees

during exposures of 30 days (Roubik 1982a, 1983). These native bees, although overlapping extensively with honeybees in diet, were generalists and Roubik suggests that they simply switched to other floral resources and so avoided serious competition. However, changes in colony performance may not become evident within 30 days or the changes may not be of sufficient magnitude to be detected within that time period. Furthermore, Roubik (1982a, 1983) suggested that the actual density of honeybee colonies used in the experiments (if their foraging range was taken into account) was probably equivalent to a density of about 1 honeybee col/km^2 and that this density may not be sufficient to elicit a significant response or properly test the impact of colonising Africanized honeybees on native social bees. Based on estimated densities for Africanized honeybees in other parts of South and Central America, densities approaching 10 feral col/km^2 might eventually establish. Subsequently Roubik *et at.* (1986) examined the foraging activity and resource harvests of 17 colonies of 12 species of native bees in the presence and absence of 20 colonies of honeybees. When honeybees were present the foraging activity for most colonies of native bees declined and for 7 of 31 cases the decline was significant. Colonies of native bees had rare and brief periods of intensive harvesting. During these peak periods up to 51% of the food being harvested by a colony was being collected in just 4% of the time that colonies were active (Roubik *et at.* 1986). For all colonies of native bees these peaks of activity were diminished when honeybees were present and as a consequence the amount of food harvested by colonies was reduced by about 25% (Roubik 1988). Roubik *et al.* (1986) estimated that at this rate some native bees may disappear within 10 years.

Longer-term studies have shown that there have been gradual increases in the proportional abundances of honeybees and decreases in native bees at flowers in Panama and French Guiana (Roubik 1988, 1991, unpubl.). In 1977, one year after honeybee arrival, honeybees accounted for 7% of bees at flowers but in 1981 and 1982 they accounted for 67% and 75% respectively (Roubik 1988). Despite this there was no abrupt drop in the numbers of native bees counted at baiting stations or caught in traps

during the -first few years after Africanized honeybees arrived in the area but careful analysis of individual species or sets of species were still to be undertaken (Wolda and Roubik 1986; Roubik and Ackerman 1987; Roubik 1988).

Again, these studies by Roubik highlight the difficulty of conducting effective field experiments that test for impacts of honeybees on native bees. Simply introducing a few colonies of honeybees to an area for short periods of time may not be sufficient to elicit a measurable response at a population level. Various behavioural strategies may allow native bees to cope with short-term or localised food losses. First, most stingless social bees in Central America forage at a wide range of plants (eg Roubik *et al.* 1986) and can probably shift to othet resources if displaced from particular plant species by honeybees. On Barro Colorado Island, Panama, Roubik and Aluja (1983) showed that individuals of two species of stingless social bee were capable of navigating back to their colonies over distances of 1.5-2.1 km. Thus stingless social bees from individual colonies may be able to exploit floral resources from areas of 7-12 km^2, providing considerable scope for avoiding areas and plant species being used extensively by honeybees. Second, these bees often store surplus resources well above their immediate needs and so can wait out periods of resource scarcity by using these reserves (Roubik 1982b) without changes in abundance taking place. Furthermore, average worker life spans may be longer during periods of food shortage (possibly because the bees are less active) reducing the rates of brood production needed to maintain colony size and presumably reducing demands on food stores (Roubik 1982b). Australian native bees may also have an ability to fast and so wait out periods of food scarcity and/or inclement weather (eg Sugden 1988).

In Germany, Evertz (1993) has examined interactions between honeybees and other species of wild bee. Three separate studies - were reported. In one study natural bee communities and population sizes of selected species were monitored at four sites over three years. Colonies of honeybees were introduced to two of the sites in the second year and the abundances of wild bees, particularly oligolectic species (eg *Andrena vaga* and *Colletes succinctus),* were reduced

along line transects in those areas with added hives of honeybees. Evertz (1993) suggests the species most affected were those whose pollen sources were harvested extensively by honeybees. In the second study, Evertz showed that the numbers of *Colletes succinctus* found in meadows increased with distance from an apiary. In the final study, Evertz (1993) introduced nesting blocks of 250 coccoons of leaf-cutter bees *(Megachile rotunda)* to areas of lucerne planted on land being reclaimed after coal mining. The coccoons subsequently hatched and Evertz then scored the number of new coccoons produced two months later in areas with and without added colonies of honeybees. In two of four separate experiments the number of new coccoons produced in areas without honeybees was twice those produced in areas with honeybees, in another it was five times higher and in the fourth there was no difference. Evertz (1993) attributed the variability in competitive response to differences in the availability of floral resources during the different experiments with competition being greater when floral resources were more limited.

Information on interactions between honeybees and other fauna and flora is scant; but two studies support some of the work conducted in Australia. Wilson and Thomson (1991) showed that extensive loss of pollen to introduced *Apis mellifera* (and *Dialictus rohweri)* reduced the quantities of pollen being deposited at the stigmas of *Impatiens capensis.* However, they did not consider whether this reduced rate of pollination led to reduced seed production. Roubik (unpubl., pers. comm.), however, has recently found that seed production for a native South American legume was reduced when feral honeybees displaced native bees from flowering patches, the displacement being most severe in slightly disturbed habitats. The results of these studies are consistent with those reported for *Callistemon rugulosus* and *Correa reflexa* in Australia (Paton 1993; and above). Other studies have also shown that nectar-robbing bees (not Apis) can reduce the frequency with which nectarfeeding hummingbirds visit flowers and lead to reduced seed production as well (eg Roubik 1982c; Gill *et al.* 1982), illustrating the potential for nectar-robbing bees to displace nectar-feeding birds and disrupt pollination processes.-

Competition between feral honeybees and hollow-frequenting native fauna

Possums, gliders, bats, some dasyurids and a wide variety of birds (eg parrots, cockatoos, some ducks, some falcons, owls, owlet-nightjars, kookaburras, kingfishers, tree martins, treecreepers) and some reptiles may use hollows in trees for roosting and nesting in Australia (Saunders 1979; Saunders et al. 1982; Pruett-Jones et al. 1980; Tidemann and Flavel 1987; Lunney et al. 1988; Lindenmayer et al. 1990a; Joseph et al. 1991; Mawson and Long 1994). Some of these species could potentially compete with feral honeybees for hollows. However, there is no strong evidence of competition between feral honeybees and any of these hollowfrequenting native fauna. Concern about competitive interactions is based largely on recorded instances of honeybees displacing cockatoos from hollows (Saunders 1979; Matthews 1984; Bell 1987; Rowley 1990) or of honeybees occupying hollows that had previously been used by bats, parrots or owlet-nightjars (Tidemann and Flavel 1987; Mawson and Long 1994; McDonald 1994). These displacements, however, may only involve a small proportion of the population and have no significant effect on the population sizes of native fauna, particularly if other hollows are available for use. For example, Rowley (1990) records only two incidences of feral honeybees displacing Galahs from nesting hollows out of some 602 nesting attempts. Similarly Saunders (1979) recorded only two cases of honeybees displacing White-tailed Black Cockatoos from their nests in over 300 nesting attempts that were recorded over six or seven years. Saunders still regarded honeybees as being a problem perhaps because they occupied other hollows that were not used by the cockatoos. Others have attempted to assess the potential for competitive interactions by estimating the likely overlap in dimensions of hollows used by selected native fauna and honeybees and/or by considering the occupancy rates for hollows in an area (Stace 1988; Wapshere 1988; Manning 1993a; Oldroyd et al. 1994).

Information on the sizes of hollows used by Australian native fauna are scant except for some information on the dimensions of nest cavities used by several cockatoos and parrots in Western Australia (Saunders et al. 1982), bats in south-eastern Australia (Tidemann and Flavel 1987) and information on the sizes of artificial nest boxes used by various mammals and birds (eg Menkhorst 1984). Unfortunately there are no data on the sizes of natural cavities used by feral honeybees in Australia and so the comparisons that have been made (Wapshere 1988, Stace 1988) have used information collected on feral honeybees in other countries.

Overseas studies have reported that feral colonies of honeybees use cavities of 10-450 L capacity though most were in the range of 20-80 L (Seeley and Morse 1976, 1978; Seeley 1977; Jaycox and Parise 1980; Rinderer et al. 1981,1982; Winston 1987; Schneider and Blyther 1988). Most of this information was based on just 21 natural nest cavities found near Ithaca, NY that Seeley and Morse (1976) cut open and measured and a further 28 nests in manmade structures that Seeley (1977) measured, although Schneider and Blyther (1988) provide comparable data for an African race of the honeybee *Apis mellifera* scutella. Other studies merely recorded the preferences of swarms when offered a limited range of different-sized cavities. These showed that swarms would use cavities that ranged in size from as little as 10 L to at least 100 L. Volumes of nest cavities for feral honeybees from overseas overlap with the volumes of nest cavities used by various cockatoos (Saunders et al. 1982) and nest boxes used by a range of possums, gliders and birds in Australia (Menkhorst 1984; McDonald 1994) but other than indicating the presence of an overlap nothing can be concluded about potential competition from these comparisons.

Although most studies have not thoroughly examined all hollows the consensus is that natural hollows in most areas are under-used. Saunders (1979) and Saunders et al. (1982) recorded rates of occupation for hollows suitably sized for various cockatoos and indicated that 29-53% of these hollows at two sites were occupied by birds (of eight species) in spring over a number of years. These data suggested that hollows were not in short supply within these breeding areas and that occupation of some hollows by honeybees would not have affected these

birds (though habitats with suitable hollow-containing trees may have been limiting). Braithwaite *et al.* (1984) examined 104 hollows in trees felled in the Eden area, NSW and reported that animals used 23 of the hollows and honeybees four, again suggesting that hollows were not in short supply. Gates (1992) recorded occupancy rates for hollows in 86 dead *Eucalyptus camaldulensis* (64) and *E. largiflorens (22)* at Disher Creek near Renmark, South Australia. Only 61 (13%) of the 458 hollows were being used for nesting by birds and a few (< 10) were occupied by bats. No honeybees were recorded. In remnant woodland in the southern Mt Lofty Ranges, South Australia, Paton and coworkers (unpubl.) examined 511 trees and recorded 137 hollows in 73 of the trees. Only one of the hollows (<1%) was occupied by honeybees. Lindenmayer *et al.* (1990a) reported that 31% of 1125 hollow trees stagwatched in mountain ash forest of the Central Highlands, Victoria were occupied by arboreal mammals but occupation rates varied from 0% to 100% of hollow trees from site to site. Many also housed bats but details were not recorded and no information was provided on the use of these trees by birds or honeybees. These forests, however, are generally regarded as being poor sites for feral honeybees (see table 2). Finally, Oldroyd *et al.* (1994) found that only 0. 7% of possible hollows and 1.3% of trees examined at Wyperfeld NP, Victoria were occupied by honeybees. No attempt was made to determine what proportion of these hollows were being used by native fauna except that Regent Parrots, *Polytelis anthopeplus* used 0. 4% of the possible hollows during spring. Oldroyd *et al.* (1994) carried the analyses a little further and concluded that 52% of the feral honeybee colonies in the area were using hollows that either had entrances that were smaller than those being used by Regent Parrots or were closer to the ground and suggested that this would help to reduce any competition between these two taxa. Burbidge (1985) concluded that Regent Parrots were more likely to be limited by food supply rather than availability of hollows.

These conclusions contrast with observations made by Frank Noelker of a reduction in Regent Parrots at Lake Albacutta coinciding with increasing feral bee occupancy of redgum hollows (R Begg pers. comm.). Over a number of years the percentage of hollows occupied by honeybees increased to 16% and over the same period 12 pairs of Regent Parrots abandoned the area. Although these observations suggest that competition for hollows between feral honeybees and some hollow-nesting fauna may exist in some areas, other factors such as changes in food supply and disease could have eliminated birds from an area.

The generally low rates of hollow occupancy by honeybees (typically < 1% of hollows and <1% of trees) reported for woodland and forested areas, however, may not be maintained in agricultural areas and other areas where the number of hollows is low. For example, Paton and Eldridge (unpubl.) examined 416 remnant eucalypts along roadways and in agricultural areas of the South East of South Australia. Ninety-three trees had hollows and eight of these had feral colonies of honeybees. Although only 2% of all the trees examined in this area had feral colonies, 9% of the trees with hollows had feral colonies. Losses of further trees, particularly the larger trees that generally contain hollows, may increase occupancy rates for feral honeybees and result in competitive interactions between honeybees and native wildlife for the few remaining hollows.

Most studies on hollow availability have simply recorded the numbers of trees above a certain diameter that contain hollows, the numbers of entrances that are present in the trees and whether hollows are being used during a short interval of time (usually a few minutes of observation time or during a brief inspection of the hollow; eg Braithwaite *et al.* 1984; Oldroyd *et al.,* 1994). The sizes of the hollows behind these entrances are rarely measured or assessed to see if they are potentially usable by different taxa. Hollow limbs and trunks may be too large, too small, lack an adequate floor and or be used-by other animals (eg bats) that cannot be determined without internal examination.

The choice of hollows for use might also be influenced by ease of access for possible predators (eg goannas, snakes) and availability of nearby perches that facilitate access for users (eg Tidemann and Flavel 1987; Smith and Lindenmayer 1988). Some hollows are also frequently used by different species of birds and mammals at different times in the year or in different years

(Saunders 1979; Menkhorst 1984; McDonald 1994) and previous use may influence subsequent use. Native fauna might also regularly avoid certain hollows and or shift hollows as part of anti-predator, anti-disease or some other behaviour (Tidemann and Flavel 1987; Lunney *et al.* 1988; Taylor and Savva 1988) or exclude other species or conspecifics from an area so not all hollows are occupied at any one time (Saunders *et al.* 1982; Menkhorst 1984; Smith and Lindenmayer 1988; Lindenmayer *et al.* 1990a). Thus a network of suitable hollows may be required by a species within an area and, although only a small proportion of them may be occupied at any one time, over a longer time period a much higher proportion of the hollows may actually be used by native fauna. Studies reporting that only a small proportion of hollows are occupied at any one time often fail to consider these possibilities and have largely assumed that suitable unoccupied hollows are surplus to wildlife requirements. This may not be the case.

Assessments of potential competitive interactions between feral colonies of honeybees and native hollow-dependent fauna are far from satisfying. Honeybees, however, occupy only a small proportion of the hollows and for this reason they are not considered to be a major problem in many of the forested areas of Australia. In fact, honeybees are not mentioned in a number of studies on hollows. Of greater concern is the continuing loss of old hollow-bearing trees due to logging of forests, clearing for agriculture and natural decay without replacement (Saunders 1979; Saunders *et al.* 1982; Smith and Lindenmayer 1988; Lunney *et al.* 1988; Lindenmayer *et al.* 1990a,b; Joseph *et al.* 1991; Bennett *et al.* 1994; Nelson and Morris 1994; Mawson and Long 1994; Gibbons and Lindenmayer 1995). There are no overseas studies that have examined possible competitive interactions between feral colonies of honeybees and other hollow-frequenting fauna.

Summary and general discussion

Honeybees interact with a wide variety of Australian plants and animals, with records of honeybees working the flowers of at least 200 Australian plant genera. For many plants, honeybees are now the most frequent floral visitors, often consuming more than half of a plant's floral resources. As such honeybees interact significantly with the Australian biota and these interactions need urgent assessment.

A few studies have attempted to measure the impacts of honeybees on native fauna and flora. Studies on native bees suggest their abundance at particular flowering plants is reduced when honeybees are working the flowers but data presented to support this are equivocal. Furthermore studies on reproductive parameters of several species of Australian native bees have so far failed to demonstrate a conspicuous and consistent negative effect. However, these studies may have failed to manipulate honeybee densities adequately to cause a measurable response and second order interactions involving responses by predators or parasites may have confounded the response of native bees. Future studies will need to pay greater attention to the spatial and temporal scales of any experimental studies, and to the type (addition versus removal of honeybees) and magnitude of any manipulations.

The responses of honeyeaters to introductions of honeybees varied. In areas like Ngarkat CP where there were surplus resources during the winter, numbers of honeyeaters did not decrease following the introduction of commercial loads of honeybees. In this particular case some resources still remained unexploited at the end of the day even at sites stocked with honeybees. In other areas where there were no surplus resources individual honeyeaters often held feeding territories. Territorial honeyeaters responded to losses of nectar to honeybees by increasing the sizes of their feeding territories and adjusting the frequency with which they visited particular flowers. Increases in territory sizes of 30-50% reduced population densities by 30-50%. However, whether losses of up to a half of the birds living in an area are critical to the long-term persistence of these honeyeaters is not known. Future work will need to establish if

these localised reductions threaten the long-term viability of these birds. Presumably there have been competitive interactions between the birds and bees for approximately 100 years, although the intensity and frequency of this competition may have increased over the last 30-40 years with continued habitat destruction and degradation, and substantial increases in the numbers of managed colonies of honeybees in Australia. Because the birds have survived these past perturbations, they appear not to be threatened. The impact of competitive interactions, however, may be more complex than just the simple exclusion of part of the honeyeater population. Females appear to be displaced more frequently than males and this may affect population dynamics. Further work is required.

Honeybees also influence the production of seeds by various plants. Their presence reduces seed production and/or rates of pollination for several predominantly bird-pollinated plants. Other plants experience enhanced production when honeybees are present. Plants experiencing increases in seed production appear to be those that are pollinator limited, suggesting that native fauna are no longer providing an adequate service. Plant-pollinator systems are potentially vulnerable to perturbations like habitat clearance and degradation (Rathcke and Jules 1993) and honeybees may now be important pollinators of native plants in small remnants where native pollinators are deficient (eg Aizen and Feinsinger 1994). Reported and suspected incidences of pollinator limitation in Australian plants largely involve plants, including *Banksia,* that flower during winter or spring and are pollinated to some _extent by birds (Paton 1988; Copland and Whelan 1989; Vaughton 1991; Whelan and Goldingay 1986, 1989; Goldingay and Whelan 1990). Frequent observations that floral resources are-more abundant during the winter months than during summer months are consistent with this pattern. Several species of eucalypts may also experience shortages of pollinators particularly in plantations and so benefit from attention by honeybees (eg Loneragan 1979, Moncur et *at.* 1993). These differing responses by the plants need to be considered before implementing management programs for honeybees.

Feral honeybees use hollows that broadly overlap with those that are used by a wide variety of birds and mammals. Initial studies suggest that honeybees only occupy a small proportion of available hollows (often <1%) and that interactions with hollow-nesting fauna may not be substantial. However, few studies make an adequate assessment of the availability of suitable hollows (including internal characteristics) and-in some locations where hollows are rare, significant competition may occur.

4. MANAGEMENT OF HONEYBEES IN THE AUSTRALIAN ENVIRONMENT

General background

Land-managers in Australia are left in a dilemma about whether honeybees should or should not be managed in areas set aside for conservation and, if managed, what management actions are required. Their dilemma reflects a lack of adequate information on the biology of most native taxa and insufficient information on how these taxa are being affected by honeybees. In the few studies that have been completed, the impacts of honeybees on natural systems have varied from reducing honeyeater populations and reducing seed production in some plants to having a negligible effect on native biota or even enhancing the seed production of a number of other plant species. Such a range of responses is not unexpected.

Interactions between honeybees, and native flora and fauna are complex and diverse. Not only do honeybees interact with a great diversity of flora and fauna at any one time and in a substantial way, but the native plants and animals also interact amongst themselves. As a result consistent negative or positive responses to honeybees across all taxa in all years are unlikely. Furthermore, most natural environments in Australia have been perturbed to some extent since European colonisation. As a result many of the natural interactions within these remnant systems may have changed, even irreparably damaged. Plant-animal interactions are particularly sensitive to perturbations since only one of the partners needs to be affected for both to suffer (eg Ford and Paton 1986; Rathcke and Jules 1993). Habitat fragmentation and degradation are the most significant perturbations affecting Australian flora and fauna (eg Saunders *et al.* 1990) but honeybees too may have played a role. Past perturbations may have forced some Australian plants to depend on honeybees for full pollination because their native pollinators have declined dramatically or disappeared in some areas (eg table 19; Paton

1993, unpubl., Aizen and Feinsinger 1994). Other plants and animals, however, may continue to decline in the presence of honeybees. The eventual decisions on whether to include or exclude honeybees from an area will depend on which native taxa are to be favoured in that area.

The management of honeybees is even more challenging than this. Land managers need to consider:

1. both feral and managed populations of honeybees;
2. the economic ramifications to the beekeeping and horticultural industries of excluding or further restricting access of commercial beekeepers to selected areas;
3. implementing buffer zones several kilometres in width around sensitive areas to effectively exclude honeybees; and
4. integrating management actions both on and off reserves.

Current and future approaches to management

Rules and regulations have been implemented in different states to control various aspects of the honeybee industry and to set a code of behavioural standards for beekeepers. Most of these rules and regulations are designed to minimise accidental spread of various bee diseases, weeds and plant pathogens like *Phytophthora,* or to minimise physical disturbance at apiary sites or hazards to the general public. These regulations largely operate through the primary industry and environment portfolios of each state. Current management of honeybees in areas set aside for conservation consists mainly of restricting or managing access by beekeepers. In most cases this has involved limiting the access of beekeepers to specific sites where apiaries can be placed within reserves, with little or no restrictions on the time of the year, the length of time or the numbers of hives that

can be placed at a site. Little effort is spent on controlling feral colonies of honeybees in conservation areas.

Although states currently have some control on whether managed hives should be placed in a particular reserve or not, they have negligible control over the placement of apiaries on private property immediately adjacent to a reserve. Honeybees can readily harvest resources up to 2 km from their hives, so effective exclusion of managed hives from a reserve will also require apiaries to be excluded from a relatively wide buffer zone around a reserve. Since enacting legislation that prevents apiaries from being placed on land adjacento to a reserve will be difficult, effective exclusion of honeybees from a reserve will depend on the goodwill of beekeepers. Most states regularly review their policies on beekeeping in reserves and these reviews largely involve re-assessing whether managed honeybees should or should not be permitted in reserves because of impacts on wildlife or the lack of them. Some states, notably Queensland, New South Wales and the Northern Territory, are considering phasing out and/or banning beekeeping from nature reserves, justifying this on the belief that endemic flora and fauna will benefit if alien taxa including honeybees are excluded from conservation areas. In other states continued access for beekeepers to `traditional' resources within reserves is likely to continue but no expansion. In this case the justification is a belief that the continued presence of honeybees in conserved lands will cause no further permanent damage. Neither belief is likely to hold true in all situations and as a consequence both policies are open to criticism.

The management of honeybees will remain contentious while there is insufficient information on the effects of honeybees on Australian biota. Since obtaining sufficient information will be time consuming, alternative approaches to management that do not depend on evidence of impacts should be considered.

Realistically the exclusion of managed honeybees from all reserves will be difficult for a variety of reasons, both practical and political. Furthermore in some areas the inclusion of honeybees within a reserve may be required for the maintenance of certain plant species that may have lost their native pollinators. Given the recent emphasis on the conservation of biodiversity at a regional scale, an alternative approach would be to manage honeybees in such a way that at least some areas of natural resources within each region are maintained entirely free of honeybees (for those regions where honeybees are already present). This would at least promote diversity in these regions with interactions between Australian biota and honeybees ranging from no or negligible interaction at some locations to a variable level of interaction at other locations.

Such an approach to managing honeybees would need to be developed in cooperation with the honeybee industry. The first step should consist of developing a core strategy that can be applied nationally that is also mutually' acceptable to both land managers and beekeepers. Agencies like the Australian Nature Conservation Agency would have a key role in facilitating this.

The following is given to illustrate possible key components of a core strategy but note that the statements given are not intended to be either exhaustive or to pre-empt alternatives.

(1) Managed honeybees should be excluded from all reserves that have had no history of regular use by beekeepers.

(2) Continued access for beekeepers to conserved resources without expansion should be permitted in reserves that have had a history of regular use by beekeepers, provided that:

   (i) the extent of use of natural resources in the region does not exceed the value set in statement 3 (below);

   (ii) there is <u>no specific evidence for that reserve</u> that shows that continued use is detrimental to natural processes; and

   (iii) if research shows a detrimental effect then methods of reducing that impact by adjusting apiary size, spacing of apiaries and timing of use must -be assessed before negotiating with beekeepers a strategy for reducing access.

(3) At least 30% of the natural resources that remain within each biogeographic region should be free from exposure to managed honeybees (note that the 30% is only illustrative, and a higher or lower value could be agreed to). Where less than 30% is free from managed honeybees a mutually agreed program of reducing the level of use within a certain time period (eg 5 years) be negotiated with the beekeeping industry.

One advantage of such an approach is that management actions are based entirely on the area of land within a region that is exposed to honeybees and not on whether the interactions are detrimental or not to natural systems. The approach provides some protection for natural systems from honeybees while still allowing beekeepers access to natural resources in other parts of a region. Natural resources both on and off reserves can and should be included in this program. Although the above does not include feral populations of honeybees, a similar set of statements could be developed and incorporated into the above to guarantee that a proportion of the natural systems of a region are also free of feral honeybees.

There will clearly be some debate about the scale of these management programs, the proportion of natural resources that should be free of honeybees, and how the area of natural resources exposed to managed honeybees should be determined. Initially management of honeybees could be examined at the scale of the regions defined by the Interim Biogeographical Regionalisation of Australia (IBRA), and then subsequently at a finer scale, perhaps subunits (eg habitat types) within IBRA regions. Something approaching a 2 km radius around each apiary could be used to estimate the area of natural resources exposed to managed honeybees within a region in the first instance. In due course a more sophisticated approach could take into account stocking rates (apiary size, length of tenure) and eventually stocking rates might be adaptive, being adjusted, perhaps annually, to changes in local floral densities (eg see Paton 1990).

Such an• area-based regional approach may also help to direct future research, with research being concentrated in those regions experiencing the most extensive exposure to honeybees. One of the immediate research programs might involve compiling statistics on the distributions of managed and feral populations of honeybees within regions to assist in identifying those regions where negligible areas of natural resources are free from honeybees. These regions should then be targetted for research and management. This should consist of developing acceptable methods of reducing the area over which honeybees interact with the natural systems of the region, implementing these actions, and measuring the biotic responses to them.

5. FUTURE RESEARCH

Introduction

Effective management of honeybees in natural systems will eventually depend on accumulating sufficient information on:

1. the biology of most of the native taxa that now interact with honeybees and whether those taxa suffer or benefit from the interaction;
2. the ecology of feral and managed populations of honeybees; and
3. efficient and effective ways of removing feral colonies of honeybees from areas.

Future research needs to address each of these.

Modern ecological approaches demand manipulative experiments to test for interactions between taxa and to assess the benefits of various management actions. Wapshere (1988) outlines some of the manipulative experiments needed to test hypotheses concerning the effects of honeybees on native flora and fauna. Manipulative experiments, however, cannot be designed or executed without some knowledge of the systems in the first place and so descriptive studies will often need to precede experimental studies. Descriptive studies are particularly important in that they allow appropriate temporal and spatial scales to be determined for experiments as well as providing information on the inherent variability within these systems. Knowledge of that variability allows adequate levels of replication to be set for experimental studies. Examples of the types of descriptive and experimental studies that are needed are given below and include an outline of the methods and a discussion of the factors that need to be considered when designing field experiments. For convenience these studies are grouped under five headings:

1. Research on interactions between honeybees, flower-visiting fauna and flora.
2. Studies of hollow use by native fauna and honeybees.
3. Studies on the population dynamics of feral honeybees to identify limiting factors.
4. Research on the efficacy of various techniques to control or eradicate feral honeybees.
5. Studies on patterns of floral resource production and use of these resources by commercial beekeepers.

Research on interactions between honeybees, flower-visiting fauna and flora *Selecting taxa for study*

Several criteria could be used to select taxa for study. The first and foremost criterion should be that the taxon interacts with honeybees. Given that a great diversity of taxa interact with honeybees then a representative range of plants and animals should be selected for study, since any one or all of these taxa may be affected, and/or affected in different ways. Paton (1993) suggests a further refinement. Specific taxa should be selected based on the magnitude of the interactions that are taking place, the magnitude of an interaction being judged by the frequency with which honeybees visit flowers and/or by the proportion or quantities of floral resources that are being consumed by honeybees (eg tables 6,7). When a large share of the floral resources of a plant are being consumed by honeybees a significant impact on either the plants or native fauna is more likely than when only a small proportion of the resources are being consumed. This approach to selecting taxa for study is different to that promoted by most conservation agencies where the focus is on endangered, vulnerable or rare taxa irrespective of the level of interaction. Thus the first stage involves identifying those plants that are being heavily exploited by honeybees. Methods for doing this are outlined in Paton (1990) and are not given here.

Certain other features can also be used to select from this list those taxa that are more likely to be affected by honeybees, The following additional criteria are likely to make certain plants and animals more sensitive to perturbations from honeybees.

Plants that are obligate outcrossers, have large floral displays and are widely spaced are more likely to be affected detrimentally by honeybees than those that are selfcompatible, have small floral displays and occur in dense aggregations. This is because individual honeybees tend to forage in restricted areas and are less likely to move between plants when the floral displays and the distances between plants are large. Plants that require particular animals to operate the pollination mechanism may also be more susceptible than those that have less specialised flowers that can be pollinated by a range of animals (including honeybees). At present only limited information is available on the reproductive biology of most of the native plants that interact with honeybees. Whether any of these plants depend on particular native fauna for pollination is also often not known.

Selecting appropriate fauna for study is more complex than that for plants because there are usually several to many species of native animals visiting each of the plant species that honeybees might be using extensively. Competition for floral resources, however, is likely to be more severe for native animals that are larger rather than smaller than honeybees. Larger species have greater demands for food resources than smaller species (all other things being equal) and so are more likely to be affected detrimentally if resources at flowers are more heavily cropped. Thus vertebrates may be more sensitive than invertebrates to the foraging activity of honeybees. Other factors that may be important include the time of the day when an animal forages and how this relates to resource availability at flowers, and whether or not the animal specialises on only one or a few key plants and whether these are used extensively by honeybees.

Wapshere (1988) suggests that native bees of the genus *Trigona* should be studied since these bees are social and hence more similar behaviourally to honeybees than other native fauna. However *Trigona* are usually much smaller than honeybees and so may not overlap extensively in foraging niche. Others would argue that the largest (>I 0 mm in length) native bees (eg species of *Lestis)* are more likely to be affected by losses of food resources to honeybees since their food requirements are greater than smaller native bees, or the short-tongued bees because access to nectar is more restricted for them. Previous workers, however, have selected species of native bee that are relatively well-known and whose reproductive performance can be measured (eg species of *Exoneura;* Sugden and Pyke 1991; Schwartz *et at.* unpubl.) yet these species may not have overlapped extensively in foraging niche with honeybees. A large body of data shows that a wide variety of taxa including birds, native bees and other invertebrates all interact significantly with honeybees and any one of these could be adversely affected by them.

A range of plants and animals that interact with honeybees should. be selected for study.

Studies on the plants

For the plants involved in significant interactions with honeybees the first suite of studies should document the plant's reproductive performance. This should consist of:

1. establishing the breeding system of the plant;
2. measuring the current rate and variability in seed production both across the flowering season and between individual plants of the same species; and
3. determining if seed production is limited by pollination..

These basic measurements are important for establishing sample sizes and levels of replication in subsequent experiments and for providing direction for the next stage of the research. For example, if the conversion rate of flowers to fruits is highly variable then more replicates of each of the treatments may be required and a larger number of individual plants may need to be treated within each replicate to provide adequate statistical power to properly test the effects of certain factors (ie honeybees).

To a large extent if the reproductive performance of a plant is not limited by pollination thenconcerns that honeybees are having a significant detrimental effect on this plant are diminished (at least with respect to the quantity of seeds being produced). However, depending on the frequency with

which native fauna visit flowers, these plants may now depend on honeybees for seed production. Some initial assessment of the likelihood of this can be made by calculating the frequency with which native fauna visit flowers. If their visitation rates are low then the plant's dependence on honeybees for pollination may be high. For those plants where seed production is limited by the amount of pollination then further examination of the interactions between this plant, honeybees and native pollinators is warranted. This might involve recording the foraging behaviour of different floral visitors and assessing their value as pollinators. For example, observations might reveal that honeybees only visit male-phase flowers and rob flowers of nectar or pollen without effecting pollination or rarely move between plants and so differ from native pollinators in the pollination services they provide.

In both cases the only way to establish the role that honeybees are playing in their pollination is to exclude honeybees from plots and record seed production in areas with and without honeybees.

Eventually studies that measure the `quality' (genetic diversity) of seed crops may need to be implemented, but the technology for this and value of doing this depends on more detailed knowledge of the plant's pollination biology.

Studies on native fauna that visit flowers

A good understanding of the basic ecology of floral visitors is required before impacts of honeybees can be assessed. Except for some honeyeaters and a few species of native bees, these basic ecological data are lacking. Many species of invertebrates are still to be formally described, let alone studied ecologically. For example, there are an estimated 3000 species of native bees in Australia (Michener 1970; T Houston pers. comm.) of which less than 2000 have been described. Simple information on the distribution and abundance of most species of flower-visitor is urgently needed, and research on the ecology of individual species, on communities of flower-visitors and on interactions between species should be encouraged and promoted.

The usual assumption is. that honeybees interact with native flower-visiting fauna by competing for floral resources and that, this leads to a reduction in the numbers of native animals living in an area. This suggests that food resources rather than some other factor (predation, parasites, weather, nesting habitats) limits the survival and reproductive outputs of these animals. Ideally the importance of each of these factors needs to be assessed as far as developing management programs for particular fauna are concerned. However, a more strategic and focused approach is required to assess impacts of honeybees. Impacts of honeybees ultimately should be measured in terms of changes in population sizes of native fauna in response to changes in numbers of honeybees. However, measuring the population sizes of floral visitors living in an area is fraught with difficulty, particularly for highly mobile animals like floral visitors. Consequently accurate estimates of the numbers of floral visitors living in an area are often impossible to gather. Furthermore many invertebrates are small, cryptic and often difficult to see and identify, even when foraging. Some other parameters are therefore needed for assessing potential impacts.

If floral resources are limiting at a particular plant species and honeybees start to exploit those resources more extensively, then that should reduce the quantities of food being harvested from that plant by native animals, and should change the numbers of native fauna using that plant and/or change their foraging behaviour. Thus the first step in assessing impacts of honeybees on native flower-visiting fauna should be to determine if the quantities of floral resources that native flower-visitors are harvesting from plants changes with changes in honeybee numbers at flowers. If consumption of floral resources by native fauna declines with increases in honeybee numbers then that indicates a competitive interaction. Such calculations also permit some estimate of the extent to which the population sizes of native fauna might be reduced. For example, if the share of resources for one species changes from 30% to 15% then population sizes of this species should decline by 50%. Within a community of many interacting species, the share of resources may actually increase for some populations and decrease for others in the presence of honeybees but the overall share of resources for native fauna declines.

Estimating the quantities of nectar and pollen being consumed by different fauna involves measuring the nectar and pollen contents of flowers at different times of the day, determining the frequency of flower visits by different taxa throughout the day (and any patterns with respect to use of different floral stages), and measuring the quantities of nectar and/or pollen that each removes during a visit to a flower. More detailed descriptions of methods are provided in Paton (1982a, b, 1985, 1986, 1990, 1991, 1993).

The second stage of the assessment process should document the effect of food losses on population sizes, reproductive performance and/or behaviour of native fauna. Some of this is covered by the methods used for recording changes in resource consumption. For example, to estimate food consumption, the numbers of native fauna foraging at flowers, and the speed and efficiency with which they handle flowers are recorded at regular intervals throughout the day. Thus changes in the numbers of native fauna foraging at flowers (and/or the frequency with which they visit flowers) with changes in honeybee numbers are already being recorded. However, to fully assess and understand the mechanism(s) of any competitive interaction further information is often required.

Native fauna could respond in a variety of ways to food losses. They could:

1. shift to other areas that are not being exploited as heavily by honeybees;
2. switch to using other plant species not being used as heavily by honeybees;
3. increase the time they spend foraging to partially compensate for reduced food availability;
4. alter the time of the day when they feed;
5. consumeless food and loose condition;
6. reduce their requirements for food (stop feeding, aestivate);
7. produce fewer offspring, smaller offspring and/or cease to reproduce; or
8. die.

Some of these additional parameters should - also be measured but what is measured will depend on: the species being studied; the status of the population at the time of the study (eg some populations will not be reproducing at the time of the experiment in which case reproductive parameters cannot be measured); and the ease with which these parameters can be scored for a particular species. In some cases detailed observations on marked individuals will be required and this can be difficult for some species. For example, most Australian native bees are small, fly rapidly, are difficult to mark and track, and are easily disturbed when foraging. Added to these technical problems will be considerable variability between individuals which can only be countered by relatively large sample sizes. Similar types of problems will exist for other taxa.

One of the main reasons for these additional assessments is to allow the severity of any interaction to be better understood. For example, if the numbers of a particular taxon decline at a plant following increases in honeybee numbers then that decline could be from mortality or emigration, or simply from native fauna switching to other resources. Shifting to other resources or to other areas is a less extreme response than mortality. Establishing if all or only some individuals within a population of native animals are affected is also important. For example, competitive interactions with honeybees could result in some individuals within a population being excluded from an area while others remain and experience no reduction in their access to resources. Those that remain may increase their foraging activity such that counts of native fauna at flowers before and after an increase in honeybee activity remain similar, suggesting no change in numbers of native fauna. If the impact of honeybees was then measured in terms of reproductive rates (number of offspring produced per adult remaining) or as body condition (body mass) then little difference between control and experimental sites in these parameters might exist as well, since the remaining adults still have the same quantity of resources available to them. The conclusion drawn from such data would be that there was no significant effect of honeybees on this population, yet the numbers of adults remaining at the experimental site(s) had actually declined as had their total share of resources. If, however, the individual animals were marked and records kept of the numbers of marked animals resighted before and after an increase in honeybee activity, this reduction

in numbers should be detected (ie significantly fewer marked animals would be resighted at experimental sites compared to control sites). Recording foraging activities of some of these marked individuals would also detect increases in their foraging activity at the experimental sites and indicate further the significant effect of honeybees. Thus conclusions reached from studying interactions between honeybees and native fauna may differ depending on which parameters are measured.

This hypothetical case illustrates the difficulty in measuring impacts of honeybees on native fauna and the need to measure a suite of parameters if valid conclusions are to be drawn. Studies should first establish that consumption of floral resources by honeybees reduces the quantities of food available for native fauna and then establish how this loss of food influences various components of the foraging behaviour, condition, abundance and/or reproductive performance of native fauna.

Experimental manipulations

When ecologists test for an effect of honeybees on the abundance, behaviour and reproductive performance of native biota, they usually introduce a number of hives to one or more experimental areas and compare responses of plants and animals near these introductions to those of plants and animals distant from them (control areas). In many cases there is already a background level of honeybees present and the introduction of further hives of honeybees may not result in any significant increase in the numbers of honeybees foraging on the target plant in the experimental plots (eg Schaffer et at. 1983). Honeybees from individual hives often forage widely and out to distances of at least 2 km from their hives. This is equivalent to a minimum area of at least 12 km^2. Furthermore these bees may not be evenly distributed over this area (eg Visscher and Seeley 1982). Conceivably then, the introduction of ten hives to an experimental area may not increase the effective hive density in a region by more than 0.8 col/km^2 (0.008 col/ha) and not result in a substantial increase in resource consumption by honeybees in the experimental plots. If control areas were nearby (even within 5 km) then these too could conceivably experience increases in honeybee activity similar to the experimental areas.

An added problem with these experimental manipulations is that simply increasing the numbers of honeybees working flowers may not lead to any significant increase in the quantity of food harvested by honeybees, particularly if honeybees are already removing a large share of the resources. For example, relationships between the consumption of floral resources and numbers of honeybees working flowers may not be linear (eg Figure 2). When honeybee densities are low small increases in the numbers of honeybees working flowers may lead to substantial increases in the share of resources that they harvest. However, when numbers are high further increases in the numbers of honeybees working flowers may only result in negligible increases in the quantities of resources that honeybees consume. Thus, simply adding hives to an area may not cause any significant increase in competitive interactions. Before drawing any conclusions from manipulative experiments, ecologists need to show that those manipulations have actually worked and influenced the share of resources being secured by native fauna. So far, few studies have done this.

Given that future management of honeybees is either going to maintain the current levels of honeybees in conservation areas or attempt to reduce them, experimental manipulations to measure effects of honeybees on native flora and fauna should probably consider removing honeybees from an area rather than adding more hives. Although managed hives can (in theory) be excluded from sensitive areas and from surrounding buffer zones, techniques for removing feral colonies of honeybees from such a wide area are poorly developed. Thus, reducing the numbers of honeybees working flowers over a wide area is not possible at present. However, honeybee numbers can be reduced over smaller areas simply by trapping and removing honeybees that visit and attempt to forage at flowers in experimental plots while not doing this for control plots. In most cases after an initial period of removing honeybees, the numbers of honeybees arriving at these experimental plots declines. This initial decline happens because individual honeybees usually return to forage in the same patch of flowers and once these regular visitors have been removed the numbers of honeybees arriving

Figure 2. Models of the quantities of nectar and pollen removed by honeybees from *Eucalyptus cosmophylla* (a) and *Correa reflexa (b)* respectively as a function of the numbers of honeybees and honeyeaters visiting flowers. In both models the amounts of resource consumed by honeybees are plotted for three levels of bird visitation (5, 10 and 30 visits/flower/day for E. *cosmophylla* and 0.5 1.5 and 2.5 visits/flower/day for *C. reflexa).* In these models the proportions of floral resources not taken by honeybees were taken by birds. The models are based on observed patterns of visitation, measured efficiencies of nectar or pollen removal from flowers for honeybees and birds, and take into account diurnal patterns for nectar secretion or anther dehiscence. Details of these measurements and assumptions used for these models are given in Paton (1990).
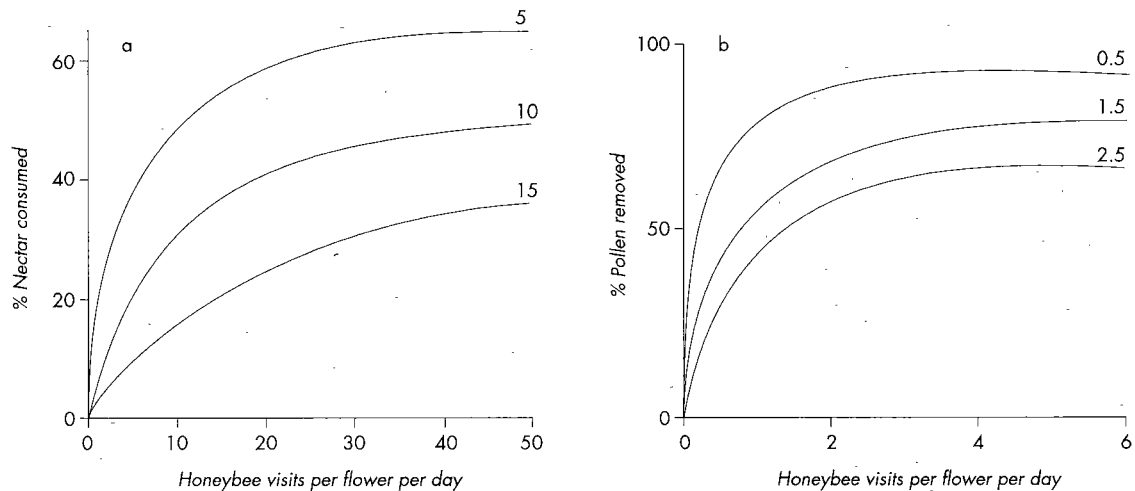
at plots is greatly reduced (Paton pers. obs.). New honeybees, however, continually recruit to patches of flowers but usually in small numbers, so some vigilance is required to maintain an area relatively free of honeybees.

Spatial and temporal scales

The other major problem in assessing impacts of honeybees on native flora and fauna is the length of time that native fauna require to respond to changes in honeybee densities and the size and distance between replicate plots. These spatial and temporal scales are always difficult to define, are likely to differ from taxon to taxon and differ with the type of experiments being attempted (removal versus addition of honeybees). For example, most solitary native bees probably forage within a few hundred metres of their nests (eg Donovan 1980), although hard evidence for this is lacking. If so their performance in an area is influenced by changes in resources at that scale. However, the numbers present in one year may be determined by conditions in the previous year since those conditions will determine the numbers of eggs that were laid, the

quantities of food provided for larvae and the numbers of adults that subsequently emerge. Thus any impacts of honeybees on native bees in one year may not be expressed until the next generation -of adults emerges.

The foraging range of honeybeesadds a further dimension to the problems of spatial scales. Although individual honeybees may forage in relatively well-defined and small areas that are possibly smaller than the areas used by individual native bees, honeybees from a single hive collectively forage over a wide area. As a result honeybees are likely to be influenced by the availability of resources over an area of at least 10 km^2 and potentially up to 300 km^2 when conditions are poor. Independent replicates therefore often need to be at least 2 km, if not further; apart. Spatial scales may be even greater for mobile species like honeyeaters which may move on a regular basis over hundreds or even thousands of square kilometres. Their abundance and behaviour in an area may be influenced by the availability of resources in that area as well as by the availability of complementary resources in distant areas at the same or

other times of the year. Executing manipulative experiments and measuring responses of native fauna at these larger landscape scales, however, will be difficult and a commonsense approach to setting spatial and temporal scales for experiments is required. For plants the appropriate minimum spatial scale is probably determined by the neighbourhood sizes of the plants. Spatial scales for studies on native fauna are more difficult to define and so a range of spatial scales should probably be considered. Minimum sizes of experimental plots should probably exceed the area that an individual usually uses when harvesting its food requirements at the time of the experimental manipulations. .

As far as temporal scales are concerned, studies should be conducted over several years to account for year to year variations in production of floral resources by different plants, weather conditions and other potentially limiting factors (predators, parasites, pathogens).

Use of hollows by native fauna and honeybees

Potential competition between honeybees and native fauna for hollows has largely been assessed by recording the proportion of hollows that are occupied by different fauna including feral colonies of honeybees at one particular time. The -usual conclusion from these studies is that only a small proportion of the available hollows are occupied and therefore that honeybees were not displacing other hollow-nesting fauna from an area (eg Oldroyd *et al. 1994).* However, most of these studies fail to provide adequate information on the internal characteristics of the hollows being used by different animals, on patterns of use of hollows through time, and/or any relationships between attributes of different hollows and the performance of native fauna to confidently eliminate competitive interactions (the work of Saunders *(1979)* and Saunders *et al. (1982)* being exceptions). A more detailed and rigorous approach is now required to properly document the availability and use of hollows by honeybees and native fauna in a region. These also need to be supported with experimental studies that test for any negative effect of honeybees on hollow-frequenting fauna.

Three types of descriptive studies are warranted:

1. studies on the population ecology of the hollows themselves;
2. studies on the patterns and dynamics of hollow occupancy in a region; and
3. studies on the ecology of specific hollow-frequenting fauna.

Each type of study has a different focus. The first focuses on hollows and is concerned with providing information pertinent to the management of hollows in an area. Amongst the questions that need to be answered are: How many hollows are present in an area? How do they differ in size and shape? How do the numbers, sizes and shapes of hollows change through time? At what rate are new hollows being formed and hollows of different sizes and shapes being lost (eg branch fall, tree fall, tree removal, natural decay)? Studies on the patterns and dynamics of hollow-occupancy are aimed at documenting the frequency with which hollows are used and any successional or temporal patterns in use. For example, hollows that have been used by honeybees may no longer be attractive to other wildlife, even after the honeybees have died or been removed. Native fauna may also only use particular types of hollows and not others, and they may or may not show strong fidelity by breeding in the same hollow in consecutive years.

These descriptive studies on hollows and hollow-occupancy should consist of

1 . thoroughly examining trees for entrances to cavities (not just making visual assessments from the ground);
2. examining, describing and measuring the internal features of each cavity (using a battery-powered arthroscope or similar device) and so truly assessing their suitability for use by different fauna;
3. recording through time the use of cavities by different animals (ie either inspecting hollows on a monthly basis (including noting presence of any faeces and nest material) or using remote sensing techniques at entrances to record use, or observing hollow trees for animal activity (eg Smith *et al. 1989);*
4. re-measuring hollows on a regular basis (ca every 3-5 years) to determine how quickly hollows change in size and shape;

5. re-examining trees for the presence of hollows every 3-5 years to determine the rate of production and attrition of hollows within an area through time; and

6. ascertaining if younger trees are still being hollowed out by termites or attacked by fungi so determining, in the long-term, the rate at which new hollows may be produced in an area (eg Mackowski 1984).

Collecting these details may be difficult if the trees are tall or in inaccessible terrain and suitable study sites may need to be selected' on logistical grounds (ie ease of access to trees). Cherry-pickers and similar mechanical equipment may be needed to gain access to the upper branches of trees to facilitate inspections of hollows, and coress made into the heartwood to assess presence of termites or fungi.

Finally, studies on the ecology of specific hollow-frequenting species should assess whether the availability of hollows or some other factor limits the population sizes of these species. In this case the focus of any research is on the particular species and not on hollows *per se.* However, the work should include identifying any patterns between the shape, size, location and orientation of hollows and the ability of occupants to survive and reproduce in those hollows (eg as Saunders (1979) has done-for White-tailed Black Cockatoos). Various species of rare or threatened cockatoos and parrots are obvious choices for these types of studies. For these birds, assessments should include identifying the factors that cause any nest failures (predation, starvation, disease, weather, desertion) as well as recording the frequency of any agonistic interactions between individuals at or near hollows. If hollows are limiting then intraspecific and interspecific interactions at hollows should occur frequently, particularly early in the breeding season. Furthermore, if hollows are limiting then some individuals capable of reproducing should not breed. Note that the presence of non-breeding birds in a population does not necessarily mean that hollows are limiting, since other factors may have prevented those birds from breeding but if the whole population is breeding then availability of hollows is unlikely to be a limiting factor. Much of this workinvolves detailed observations on individual birds to establish

if they are not breeding and to assess the quality and proximity of the food supply being used during breeding. If individual birds spend large amounts of time foraging then that is indicative of a poor quality food supply and suggests that food rather than hollows may be limiting.

The above descriptive studies are time-consuming, tedious and expensive to implement, yet these details are needed to properly assess impacts of honeybees on hollow-nesting fauna and to properly manage hollows and native wildlife in the future. Ultimately the impact of feral honeybees on hollow-nesting fauna will need to be tested experimentally but detailed information on hollow-use will still be needed to assess the outcome of these manipulations.

Two experimental manipulations are possible. The first manipulation involves removing feral colonies from some plots of woodland and not others and then recording the responses of native fauna to this manipulation. In this case the densities of native fauna using hollows in experimental plots are measured before and after the removal of feral colonies and compared with similar data collected on control plots where feral honeybees have not been removed. If honeybees have a significant ificant effect on native hollow-nesting fauna then there should be an increase in the numbers of native fauna using hollows in those plots where feral colonies have been removed. The second manipulation involves adding nest boxes of appropriate dimensions to some plots and not others and again comparing the responses of native fauna at these plots with data for control plots -where no nest boxes have been added. In both cases detailed information on the numbers of hollows being occupied by different fauna is required both before and after the manipulation. Simply recording whether native fauna use nest boxes or use the hollows that have been vacated by honeybees is not sufficient to test for competitive interactions. Native fauna may simply use these `new' hollows by chance instead of using others in the plot, and so there may be no change in the overall densities of these animals following the manipulation. A change in overall nesting densities or total numbers of hollows that are occupied is the key variable.

The temporal and spatial scales for these experiments may provide a further challenge. Individual plots may need to be large (5 ha or more in area) to provide sufficient numbers of native fauna to be able to measure their responses with some degree of statistical power, and the manipulations may need to be maintained for several years to provide sufficient time for populations of native animals to respond.

Population dynamics of feral honeybees

Studies on the dynamics of feral populations of honeybees are required to:

1. establish the factors (eg food, water, weather, hollows etc.) that limit the numbers of colonies and their sizes in different areas;
2. measure rates of turnover of colonies in an area (including patterns associated with different-sized hollows); and
3. record seasonal patterns in resource use, colony strength and survival.

Such information will be useful for implementing programs to control feral colonies of honeybees. For example, feral colonies of honeybees may be more susceptible to eradication programs when food is not abundant.

This research involves:

1. regularly searching an area for feral colonies to identify any new colonies that have established since the last search;
2. recording whether previously located colonies were still alive;
3. collecting information on the types of hollows being used by feral colonies;
4. identifying any patterns to the survival of colonies occupying different hollows;
5. identifying any patterns to the recruitment of new colonies (eg whether hollows that were previously used by honeybees were more likely to be re-occupied by honeybees than those that had not been used);
6. recording the activity of colonies (ie numbers of foraging honeybees returning per minute) at different times in the year;

7. collecting nectar and pollen samples from honeybees returning after foraging at different times of the year to determine the primary floral resources being used to support feral colonies; and
8. estimating the quantities of nectar and pollen being produced by the major plants at different times of the year and relating these to the foraging activities of feral colonies and the colonies gain or loss in strength since the last assessment.

Methods for collecting these data have been described in earlier sections of this report.

Research on the efficacy of methods to control honeybees

At present the usual method for controlling feral colonies of honeybees is to individually poison each feral colony that is found. Shelltox pest strips and other over-thecounter insecticides have all been used to some extent to kill individual colonies. This is labour intensive and not an effective method of controlling or eradicating feral colonies of honeybees over a wide area. Some efficient broadacre technique needs to be developed to help land managers remove feral colonies from sensitive areas. However, considerable research will be required before any broadacre methods can be introduced. The most likely method(s) of control will involve using baits laced with certain chemicals that honeybees take back to the hive that eventually kill the hive. There are three areas requiring research:

1. the impact of the baiting program on non-target animals both from primary and secondary poisoning;
2. the success of the baiting program in eliminating feral colonies from a region (ie what proportion of colonies within a specified distance from a baiting station are destroyed); and
3. the speed with which the baited area is recolonised by feral honeybees.

Initial research should place out attractants for foraging honeybees (eg sugar syrup, water, bran) and record the frequency with which honeybees and native fauna attend these feeding stations. The location of dispensers (eg hanging from branches, in the shade, out in the open, close to flowering plants), the type of dispenser and the

concentration of the food should all be varied to determine the conditions that are most attractive to honeybees and least attractive to native fauna. This should also include documenting seasonal patterns of attendance at feeding trays. Danka *et al. (1992)* and Scriven *(1995)* both report that when floral resources are scarce large numbers of honeybees attend feeders, and when large numbers are attending feeders other animals are excluded.

Once the best methods and times of the year to attract honeybees but not non-target animals have been identified, the next stage in the assessment process should involve assessing various poisonous chemicals for use in killing feral colonies. A range of poisons could be considered but probably acephate, dimethoate and dichlorvos or similar chemicals should be tested first (eg Waller and Barker *1981;* Williams *et al. 1988, 1989;* Woodward and Kassebaum *1991;* Danka *et al. 1992).* There are many factors that need to be considered, including the dosage used with the attractant, the quantities needed to kill feral colonies and the subsequent fate of the poison in the environment. First, the dosage cannot be too strong or otherwise foraging honeybees are killed before they have had time to return to the hive. Second, if the dosage is too low, the amount of poison arriving back at a hive may never be sufficient to kill that colony. Some initial information can probably be obtained by allowing individual honeybees to consume different doses of particular poisons inside enclosed chambers and then recording the length of time that they survive (eg Waller and Barker *1981).* Dosages that allow foraging honeybees to survive long enough to return to their hives should then be used.

Having established the optimum concentration for the poison in the baiting solution, the next stage of the assessment process should involve examining the quantities needed to kill feral colonies. Initially some trials could be performed on managed colonies of honeybees by placing quantities of the bait solution in a small but open container inside the hive-where only honeybees from that hive have access to the poisoned bait. By measuring the quantities of the poisoned bait left in the container and the quantities of poison remaining in frames once the colony has died, some measure of the quantity of poison needed to kill hives should be obtained. Some trials on feral colonies may also be possible by placing a container with poisoned bait at the entrance or near to a feral colony and recording the amounts that had been consumed before the colony died. Considerable research on developing chemical methods of controlling feral honeybee colonies (particularly Africanized honeybees) is currently being conducted in North America and some of this research will provide guidelines on dosages and quantities for some chemicals (Williams *et al. 1988, 1989;* Loper and Sugden *1990, 1994;* Danka *et al. 1992).* Danka *et al. (1992),* working in Texas and Louisiana, have recently estimated that at least *25*mg of acephate was needed to guarantee the mortality of a colony of honeybees. They also showed that this quantity could be successfully delivered if at least 100 honeybees from a colony were foraging at a baiting station when a *50%* sucrose plus 10% honey solution was replaced with one that was laced with *500* mg L^{-1} acephate for *20-30* minutes.

Depending on the chemical that has been used, there may be a risk of secondary poisoning if native animals (eg ants) scavenge dead bees, honey, wax and/or pollen from a poisoned colony (Danka *et al. 1992;* Scriven *1995). Two* assessments are required. First, the animals that are likely to feed on the remains of a feral colony need to be identified. Second the fate, concentration and stability of the poison that arrives back at a feral colony needs to be measured to determine the risk of secondary poisoning for non-target animals. Some information on the animals likely to scavenge at honeybee colonies could be obtained by recording the species that attend live colonies and colonies that have died of natural causes or have been killed by other means: Ideally the chemicals used to poison honeybees should breakdown rapidly to non-toxic substances. Samples of dead bees, honey, wax and pollen could be taken at regular intervals after the colony has been killed and assayed for any residual toxicity. Danka *et al. (1991,1992)* have measured-residues-of acephate and methamidophos from dead bees and from the honey-wax matrix of managed colonies killed with acephate and suggested that residue levels and decay trends varied greatly among colonies.

Having selected an appropriate poison and method for dispensing the poison, the final stage in the assessment process involves field trials to test the efficiency of the method in eradicating feral colonies over a broader area. This should involve:

1. determining the numbers of feral colonies present in a number of areas (see above) at various distances away from a central location;
2. attracting honeybees to a feeding table stationed at that central site;
3. having attracted honeybees to the feeding station, the poison is added to the food being provided and the bees allowed to continue to forage; and
4. the survival of feral colonies present in the various plots at different distances from the baiting station is subsequently scored.

Based on these results some indication of the numbers of baiting stations needed per square kilometre can possibly be calculated to provide a reasonable cover within a selected area. For example, Danka *et al.* (1992) found that most colonies within 200 m of baiting stations in Louisiana and Texas usually attended feeders in sufficient numbers (>100 individuals/colony) to be killed when exposed to acephate. Attendance by honeybees from colonies beyond 200 m, however, was usually not sufficient to deliver fatal amounts of acephate. These data suggest that about 10 baiting stations per square kilometre would be required at these American sites to provide reasonable coverage. The speed with which baited areas are recolonised should also be measured to assess how frequently control programs need to be implemented. Placing decoy hives with attractant lures (eg Schmidt and Thoenes 1992; Winston and Slessor 1993) in areas during the swarming season may help to restrict the rate at which feral colonies recolonise areas, as well as allowing swarms to be easily removed.

Assessment of resource use by commercially-managed apiaries

Amateur and commercial beekeepers maintain over 500,000 hives of honeybees in Australia. Commercial apiarists and some amateur apiarists shift large numbers of hives into areas to exploit 2-4 month long peaks in the flowering of key native plants. These key plants are often species of *Eucalyptus* but can also include a variety of other shrubs and small trees (eg *Eucryphia, Banksia, Dryandra)* that because of their prominence can produce large quantities of nectar and/or pollen on a per unit area basis. Beekeepers often argue that their bees simply exploit the surplus floral resources being produced. This may be the case but this use of floral resources needs to be properly assessed. First, large numbers of hives are introduced at specific locations that may result in densities of honeybees that are much higher than background densities of feral honeybees at least on a local scale and, as a result, they may have comparable impacts on resources and native taxa. Second, commercially-managed honeybees will visit not only the flowers of abundant plants, but also less abundant plants where surpluses may not exist and where specific native fauna may be severely affected. Third, there are at least qualitative differences in the magnitude of the floral peaks from one year to the next (at least as measured in terms of honey production) in many areas (eg Berkin 1987, Manning 1992) and perhaps in the timing of flowering such that the shifts of bees into and out of areas may not always match the periods of peak flowering. Furthermore, there is an assumption that there is a staggered sequence of peaks in floral resources that allows beekeepers to shift from one resource or area to another without experiencing any lean periods. Such a staggered and complete annual sequence of peak resources may not exist. Turner *et al.* (1972) in fact recommend that hives should not be shifted from one honey flow to the next but rested between flows to allow them to rebuild hive strength. Fourth, the importance of floral peaks both in supporting native fauna and in the reproductive biology of the plants is poorly documented let alone understood.

The following items need to be measured to address some of these deficiencies and to allow sensible management plans to be developed.

1. How closely do commercial beekeepers track peaks in floral resources?
2. Which plant species provide the bulk of the resources used by commercial apiaries?
3. How does the flowering of these plants (timing and intensity) vary from year to year?
4. What proportion of the floral resources produced by these plants are harvested by honeybees?
5. What other plant species are used during these peaks and what proportion of their floral resources are harvested by honeybees?
6. Is there an annual succession of flowering peaks in different areas that can be exploited by commercial beekeepers?
7. How do native flower-visiting fauna respond to these influxes?
8. How does seed production vary across the flowering season and with influxes of commercially-managed honeybees?

These initial aims simply describe the use of resources and do not aim to assess whether the commercial industry has a negative effect on the conservation values of natural areas or resources being used. This basic information is critical for selecting those - aspects where impacts are most likely (ie particular sites, times of year, primary versus secondary plant species and/or particular fauna).

Two approaches should be taken to collecting these baseline data:

1. studies that track and document the movements and resource use of a number of commercial apiaries(ists); and
2. studies that track resource production in reserved areas where commercial loads of honeybees are placed at certain times of the year.

These studies should span at least three if notfive years to document annual variation - in resource production and patterns of use. The most efficient strategy would probably involve selecting a number of apiarists who have kept accurate records of their movements and performance. From these records, 4-10 sites that are used regularly by them should be selected for study. At these sites, the quantities of floral resources being produced would be measured at regular intervals throughout the year to document the seasonal patterns in food availability. This would require determining the abundance of plants at various distances from the site where hives are placed using quadrats and random stratified sampling. Having established the density-of the plants - future work should only involve counting the flowers present on - subsamples of plants, measuring nectar and pollen production at samples of flowers, diurnal patterns to availability and the quantities being removed by honeybees and native fauna before, during and after the commercial apiaries have been placed in each of those areas. Simple techniques for assessing resource use have been outlined above. Note, however, that - because the density of honeybees may decline with distance from an apiary some measure of resource use as a function of distance from an apiary should also be attempted as part of these studies.

Three criteria could be used to assess the likelihood that influxes of commercial loads of honeybees affect native flora and fauna:

1. the quantity of resources consumed by native taxa declines when commercial apiaries are introduced;
2. the change in numbers and or behaviour of native pollinators/flower-visitors with the introduction and subsequent removal of commercial loads of honeybees; and
3. the change in production of seeds by the plants in response to the arrival and departure of commercial loads of honeybees. -

Ideally these responses would need tobe compared with similar data collected at equivalent control areas where no commercial loads of honeybees had been placed to properly test for an impact of commercially-managed honeybees on natural systems. However, even without the control areas some useful information on the likely affects of beekeepers' honeybees on natural systems would be obtained. Such information would clearly help in developing appropriate management programs to reduce potential impacts.

Integration of research projects and priorities

The research programs that have been outlined above are all beneficial to the long term management of biotic resources in Australia. However, with the current economic climate funding all of these programs is unlikely. So which research programs should be given priority and where should those programs be carried out?

Most land managers indicate that they require information on:

1. the impacts of honeybees on native flora and fauna;
2. the distribution, abundance and population dynamics of feral colonies of honeybees; and
3. methods of efficiently and effectively removing feral colonies from an area, before implementing management programs.

In most cases the areas that they would target would be those areas with high densities of feral colonies and/or those areas where there was some concern that honeybees might impact on certain rare or endangered wildlife, mainly hollow-nesting parrots and cockatoos (Regent Parrot in Victoria; Black-Cockatoos in South Australia). The only other situations where feral colonies are given some management attention are areas where feral honeybees cause problems for humans.

The numbers of feral colonies present in an area, however, is not necessarily the best criterion for selecting sites in which to do initial work. Flora and fauna in areas with low densities of feral colonies may be just as heavily affected by honeybees, if not more so, than flora and fauna living in areas with high densities. Also, available evidence suggests that most hollow-nesting fauna are not likely to be adversely affected by honeybees (eg Rowley 1990; Oldroyd et al. 1994) but the impacts of honeybees on native flora and flower-visiting fauna could be severe based on the frequency with which honeybees visit the flowers of a wide range of plants (eg table 6). On these grounds research should concentrate on documenting the impacts of honeybees on native flora and flower-visiting fauna rather than on hollow-nesting fauna. Note that where there is concern that honeybees may be impacting hollow-nesting fauna some management actions are being implemented as part of the management programs for those endangered wildlife (eg Glossy Black Cockatoo on Kangaroo Island) and so the concern is alleviated to some extent.

Opportunities to integrate several research programs in the one area should not be ignored, since this will increase cost efficiency. For example, research programs that develop techniques for baiting feral colonies must assess the efficacy of baiting programs on feral populations. This requires information to be collected on the densities of feral colonies before and after the introduction of a baiting program. Thus as part of this program some information could be collected on the types of hollows being used by feral colonies and the proportion of hollows in an area that they occupy. Studies on population dynamics of feral colonies and rates of recolonisation could be incorporated into programs measuring the efficacy of baiting programs. Furthermore, studies on the impacts of honeybees on native flora and flower-visiting fauna could be conducted in the same areas as baiting trials providing a further opportunity to experimentally test the impacts of honeybees on these taxa. These studies could also be conducted in areas where there are concerns about particular hollow-nesting fauna providing the potential for a further benefit. By concentrating and integrating research programs in a few areas the benefits of any experimental manipulations will be maximised. Which areas should be chosen is difficult to determine. There may be some benefit to working in areas with high densities of feral colonies simply because of advantages with larger sample sizes (of feral colonies) and there may also be some merit in building on the databases that have already been collected in some areas (eg Oldroyd's work at Wyperfeld; Paton's work at Flinders Chase on Kangaroo Island; or around the nesting sites of Glossy Black Cockatoos on Kangaroo Island) rather than starting entirely from scratch in new areas. The choice of areas used for study may ultimately-depend on the availability and interests of research staff willing to be involved in this type of research.

In order of priority, the areas for research each should be:

1. to promote studies that assess the impact of honeybees on native flora and flower-visiting fauna to provide a firm basis for implementing and justifying any programs of control; and

2. to develop cost effective, environmentally safe methods of eradicating feral colonies of honeybees from selected areas.

These two research areas should be given precedence but less intense studies on the population dynamics of feral colonies and on patterns of hollow use by honeybees and native fauna should be incorporated into these programs if at all possible.

Possible sources of funding for these programs include the Australian Nature Conservation Agency (Invasive Species Program, States Cooperative Assistance Program), World Wide Fund for Nature, Australian Heritage Commission (National Estate Program), various state government grants, the Australian Research Council, and the Honeybee Research and Development Council. Of these, probably only the Australian Nature Conservation Agency and Australian Research Council have the resources to provide sufficient financial support to fund these research programs adequately. The Honeybee Research and Development Council is more likely to fund projects documenting the migratory patterns and use of floral resources by commercially-managed honeybees.

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