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Biological Conservation 123 (2005) 103–112
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

# Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaeus alcyoneus*)

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Received 7 April 2004

**Abstract**

European honey bees used for commercial honey production represent a potential source of competition for floral resources with native nectar and pollen feeding insects. This study reports the results of an experiment run over two years on the impact of commercial honey bees on the fecundity of a solitary native bee, *Hylaeus alcyoneus*. Registered apiary sites were used as treatment sites (with honey bees) while control sites (without honey bees) were interspersed between. The fecundity of *H. alcyoneus* was measured using trap nests. We compared the number of nests produced, number of eggs per nest and emerging progeny mass of *H. alcyoneus* in sites with and without commercial bee hives. The number of nests produced by *H. alcyoneus* was 23% less (Wilcoxon's *T*) at treatment sites than control sites. Analysis of individual measurement intervals using ANOVA was compromised by a general lack of power. This result highlights that even though honey bees have been present in certain areas for many years, competition with native bees may still be occurring.


*Keywords:* Competition; Hymenoptera; Interaction; Fecundity; Banksia bee

## 1. Introduction

The European honey bee (*Apis mellifera*) has been introduced to a number of continents, including South America, North America and Australia. Large, economically profitable honey producing industries have been established in these regions and in Australia the beekeeping industry, not including pollination services, is estimated to be worth $63 million/yr (Rodriguez et al., 2003). For many years it was assumed that honey bees could only be of benefit to the natural ecosystem (Wills et al., 1990). However, in the last 20 years ecologist have argued that honey bees may not be effective pollinators of native plants and may be competing with native pollinators for limited floral resources such as nectar and pollen (Sugden and Pyke, 1991; Gross, 1993; Oldroyd et al., 1994; Paton, 1996; Butz Huryn, 1997).

Beekeepers in Australia transport their hives throughout the year following the flowering of various native plants and can agist up to 100 hives in one location. This agistment represents a potentially significant increase in competition with native nectarivores. Native bees in particular, which rely on floral resources for development, survival, and food for their offspring, can be prone to competition from honey bees (Sugden et al., 1996).

For honey bees and native bees to be in competition there must first be an overlap in resource use. That is, both species must be collecting floral resources from the same plant species. With this in mind, many researchers have focussed on native bee visitation rates to flowers and they have often found a decrease in

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doi:10.1016/j.biocon.2004.11.001

response to honey bees which they interpreted as a negative impact (e.g. Roubik, 1978; Schaffer et al., 1983; Pyke and Balzer, 1985; Wenner and Thorp, 1994). However, though native bees may be visiting a floral resource less often in response to honey bees, they may be able to obtain equivalent levels of resource from a different species at the same cost or they may visit the plant species at a different time or over an extended period during the day. The cost of such a change in foraging behaviour may not influence survival and fecundity, and subsequently, the long-term survival of the native bee species may not be threatened (Paini, 2004). While visitation rates may provide a relatively quick indicator to the potential for competition between honey bees and native bees, to confirm the impact of honey bees an assessment of native bee fecundity, survival or population density in response to honey bees is necessary (Paini, 2004). Few researchers to date have investigated fecundity, survival, or population density when assessing competition between honey bees and native bees (though see Roubik, 1983; Sugden and Pyke, 1991; Spessa, 1999).

This study reports the results of an experiment designed to assess the impact of commercial levels of honey bees on the fecundity of *Hylaeus alcyoneus* (Erichson) (Hymenoptera: Colletidae), a twig-nesting native bee found throughout the southern regions of Australia (Houston, 1981). Fecundity is generally defined as the reproductive capacity of an organism, i.e., the number of eggs produced by a female over its life-time which is often difficult to estimate (Allaby, 1994). In this study, we measured fecundity of *H. alcyoneus* as the number of eggs per nest, the number of nests produced and the mass of the offspring that emerge from these nests as size has been found to affect future fecundity of offspring (Honek, 1993).

Female *H. alcyoneus* construct nests from May to August with the majority of these nests containing single sex broods, though it is not known whether females share these nests or if they are truly solitary (Paini and Bailey, 2002). In addition, egg, larval, and pupal diapause do not occur and adults appear to survive from one season to the next. *H. alcyoneus* is unusual for Hymenopterans, as the male is significantly larger than the female and Alcock and Houston (1987) have suggested that the evolution of this reversed sexual size dimorphism has been driven by a resource-defence mating strategy of males, although matings have never been observed. Finally, the offspring sex ratio of this species contradicts classical Fisherian theory as it is biased toward the larger sex and the cause of this bias is unknown at present (Paini and Bailey, 2002).

## 2. Methods

The experiment was conducted in the Northern Beekeepers Nature Reserve (30°00′S, 115°05′E), approximately 250 km north of Perth, Western Australia, during the winter of 1999 and 2000. Fourteen study sites were located in a 55-km$^2$ area dominated by low heath. Seven of the 14 sites are registered apiary sites and every winter beekeepers agist approximately 100 hives at each site. These seven apiary sites were used as treatment sites while the remaining 7 sites, free of agisted honey bees and interspersed between apiary sites, were used as control sites (Fig. 1). Beekeepers, however, did not agist hives at all sites simultaneously. Consequently, sites were designated control sites until beekeepers deposited their hives. In 1999, one apiary site was not available until after week 12.

Female *H. alcyoneus* will nest in 'trap nests', drilled sections of untreated pine batons (2 cm × 2 cm × 7 cm) providing an opportunity to measure fecundity of *H. alcyoneus* in response to honey bees. Females build linear series of cells in these holes and provision them with nectar and pollen for the developing progeny.

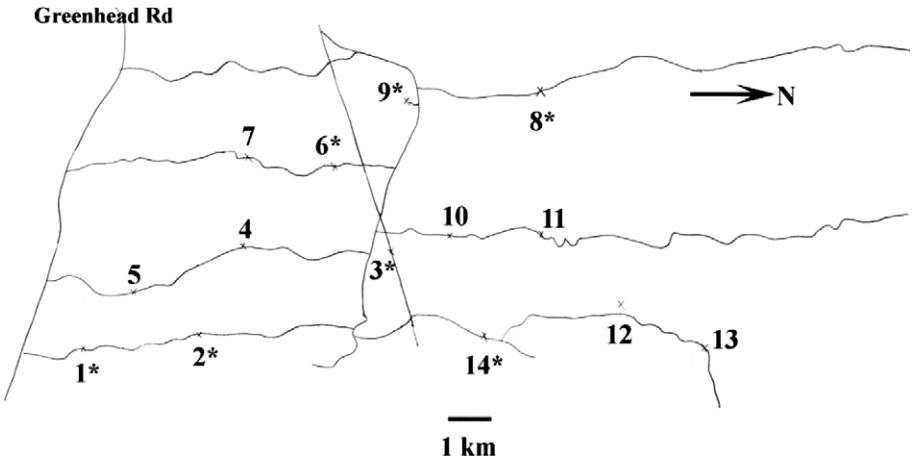


Fig. 1. Map showing the location of control and treatment sites. Treatment sites (numbers with asterisk) were registered apiary sites.

The preferred hole diameter of trap nests for *H. alcyoneus* is 7.0 mm (Paini and Bailey, 2002). A bundle (4 drilled batons tied together with wire) of trap nests was placed at 10 m intervals along two parallel transects 100 m long and 25 m apart, giving 80 trap nests per site. Bundles were hung from shrubs at a height of 10–150 cm. Trap nests were placed at 14 sites, with similar vegetation profiles at least 1.5 km apart, from April 1999 to April 2001 and checked every 3–4 weeks (measurement interval) for the presence of a septum that female *H. alcyoneus* place over a completed nest.

Completed nests were removed and replaced with a fresh trap nest. Nests were returned to the laboratory and maintained in a constant temperature chamber at 28 °C during the day and 15 °C at night. Adults emerged after 3–4 weeks and were immediately weighed. All adults that emerged from a nest were allocated to the time interval in which the nest was collected from the field. As nest construction was not monitored, it was not possible to determine if the same female laid all eggs in the one nest. In analysing progeny mass, individual eggs were therefore used as independent data points. However, the number of eggs per nest was analysed to give an indication of egg production in the population and the number of nests per site was also analysed to indicate the overall nest production.

### 2.1. Honey bee densities

Honey bee densities were assessed to ensure treatment sites had higher levels of honey bees than control sites. In 1999, inflorescences of *Dryandra sessilis* shrubs located within the two parallel trap nest transects were observed for 30 min, recording the number of honey bees present every 2 min. These counts were taken from two separate plants at each site between 10 a.m. and 3 p.m. on clear days. The numbers of mature inflorescences were noted and the honey bee counts from each two minute interval were totalled to give number of honey bees/*D. sessilis* inflorescence/site. *D. sessilis* was chosen as it was common at all sites and honey bees were known to visit this plant to collect nectar and pollen. In 2000, this regime was altered to a more efficient method. A census of honey bees was made every 10 m along both transects by scanning the surrounding area for 30 s for a total of 20 censuses (10 min). Values for each census point were totalled to give number of honey bees/10 min/site.

### 2.2. Vegetation transects

Vegetation transects were used to determine if control and experimental sites had a similar floral resource diversity. With most measurement intervals and at most sites, 50 m vegetation transects were chosen at random, though transects always ran perpendicular to and intersected trap nest transects. All flowering species that were either wholly or partly within 50 cm of the transect line, and the number of individual plants of each species was recorded. Only those individual plants that were flowering were counted. Floral resource diversity was calculated using Shannon–Wiener's diversity index $H'$ (Magurran, 1988):

$$H' = -\sum(p_i)(\log_n p_i),$$

where $p_i$ is the proportional cover of the $i$th species in a site.

### 2.3. Resource overlap

Resource overlap was assessed by comparing pollen extracted from trap nests of *H. alcyoneus* with pollen and honey collected from honey bee hives. With every measurement interval, one trap nest from each site was repeatedly and vigorously flushed with 10 ml of water to remove the pollen and larval faeces. The resulting fluid was then acetolysed following the standard technique of Erdtman (1952, 1960) (see also Phipps and Playford, 1984). The extracted pollen was preserved on microscope slides and later matched to a reference collection of pollen from plant species collected from the area.

Honey bees may collect nectar, which is converted to honey, from different plant species from those where they collect pollen. Therefore, both honey and pollen were collected from honey bee hives at each treatment site. Honey bee pollen was collected over a two-day period using pollen traps. A sub-sample (0.5 ml volume) of each pollen sample was mixed with 9.5 ml of water and acetolysed before being preserved on microscope slides. Honey was collected from hive frames. One hive frame was removed from a hive at each site and replaced with a fresh frame so any honey present was only collected in the period since the previous measurement interval. In some measurement intervals, no honey was found in the frame. Honey extracted from the frame was filtered through a container lid with holes of approximately 1 mm diameter to remove wax and then diluted by 50% with warm water. The honey/water mixture was then centrifuged at 3500 rpm for 3 min and the supernatant poured off. The remaining pellet was diluted by 50% with ethanol, heated in a water bath for 5 min to fully dissolve the honey before being centrifuged at 3500 rpm for 3 min. The supernatant was then poured off and the remaining pellet was resuspended in 9.5 ml of water and centrifuged at 3500 rpm for 3 min. This last step was repeated two more times before the pollen was acetolysed and preserved on microscope slides.

For each slide, pollen grains were counted by scanning from left to right of the slide until 100 grains were counted and the frequency of each species of pollen was calculated. Resource overlap between *H. alcyoneus* and

honey bees was then calculated according to Colwell and Futuyma (1971):

$$RO_{ih} = 1 - 1/2 \sum_{k} |p_{ik} - p_{hk}|,$$

where $p_{ik}$ is the average proportion of pollen type $k$ in the measurement interval of species $i$ and $p_{hk}$ is the average proportion of pollen type $k$ in species $h$. Values will range from 0 to 1.0 with 0 indicating no overlap and 1.0 indicating complete overlap. The difficulty in identifying pollen to species level meant that only pollen species identified from *H. alcyoneus* nests were identified in honey bee samples. Any other pollen species were classified as 'other species' as this did not affect resource overlap calculations.

### 2.4. Statistical analysis

As beekeepers did not agist hives at all treatment sites simultaneously, measurement intervals were initially analysed separately. For every ANOVA homogeneity was tested using Cochran's test and normality was tested using Kolmogorov–Smirnov goodness of fit for continuous data. Data that failed these two tests were transformed (natural log or arc-sin transformation). Heterogeneity increases the risk of a type I error which is only relevant when a significant difference between treatment and control is found (Underwood, 1999). Therefore the ANOVA was still performed on data that failed the test for homogeneity and if there was no difference between treatment and control ($\alpha = 0.05$), the result was accepted. Analysis was conducted using Statistica for Windows (Release 5.0; Statsoft Inc., Tulsa, USA). In addition, repeated tests of the same hypothesis can result in an inflation of type I error. A sequential Bonferroni test was therefore used to adjust for this bias (Holm, 1979; Rice, 1989).

Power analysis was conducted on any data that did not demonstrate a difference between treatment and control and was normal and homogenous. Power analysis estimates Type II error and was calculated from delta values for 4 alternative hypotheses (20%, 50%, 80% and 100% difference between control and treatment sites). The observed treatment effects were not used as an alternative hypothesis as they would reveal nothing about the power of the test to detect biologically important results (Thomas and Krebs, 1997; Underwood and Chapman, 2003). Power analysis assumes homogeneity plus normal distribution and little is known of the accuracy of power estimates when these assumptions are violated (Faul and Erdfelder, 1992). Data that were not normal or homogenous were transformed and if the assumptions were still violated, power analysis was not performed. Power values of greater than 0.8 indicated adequate power (Williams et al., 2001). Analysis was conducted using GPOWER (Faul and Erdfelder, 1992).

In comparisons of treatment and control sites, Wilcoxon's signed-rank test was used to determine if honey bees reduced nest production of *H. alcyoneus* over the two seasons. For this test every measurement interval from both years was treated as a randomised block. As a minimum of six randomised blocks is necessary (Sokal and Rohlf, 1995), this test was not performed on any other fecundity data.

## 3. Results

In 1999, beekeepers began agisting hives on April 19. The experiment began at this time and sites were visited and checked every three weeks. No *H. alcyoneus* nests were retrieved before week 6 (2/6/99) and after week 21 (14/9/99). In 2000, beekeepers began agisting hives on March 1. The experiment began at this time and sites were visited and checked every 4 weeks. No *H. alcyoneus* nests were retrieved before week 8 (26/4/00) and beekeepers removed their hives after week 24 (15/8/00) so the experiment was terminated.

### 3.1. Honey bee densities

For both seasons, honey bee densities were significantly higher in treatment than control sites (Fig. 2). The honey bee density data from week 24 (15 August 2000) failed Cochran's test for homogeneity, even after transformation. The heterogeneity was caused by a large number of zero values in control sites invalidating the use of analysis of variance models. However, the difference between control and treatment sites in terms of honey bee densities for week 24 was clear (Fig. 2).

### 3.2. Vegetation transects

ANOVA revealed no difference in flowering diversity between control and treatment sites within each interval period in which flowering vegetation data were recorded (Fig. 3). Data from week 12, 1999 revealed a $p$ value of 0.01. However, after adjustment using sequential Bonferroni, the test was not significant ($p$ is greater than the sequential Bonferroni adjusted value of 0.006).

### 3.3. Resource overlap

Pollen residue from *H. alcyoneus* nests at both treatment and control sites was composed entirely of *Banksia sphaerocarpa*, whether honey bees were present or not. *Banksia sphaerocarpa* pollen was also found in honey and pollen samples from honey bee hives in every measurement interval in which honey and pollen was able to be analysed (weeks 6–18 in 1999 and weeks 16–24 in 2000). Resource overlap between *H. alcyoneus* and honeybees varied between 0.52 and 0.97 (Table 1).

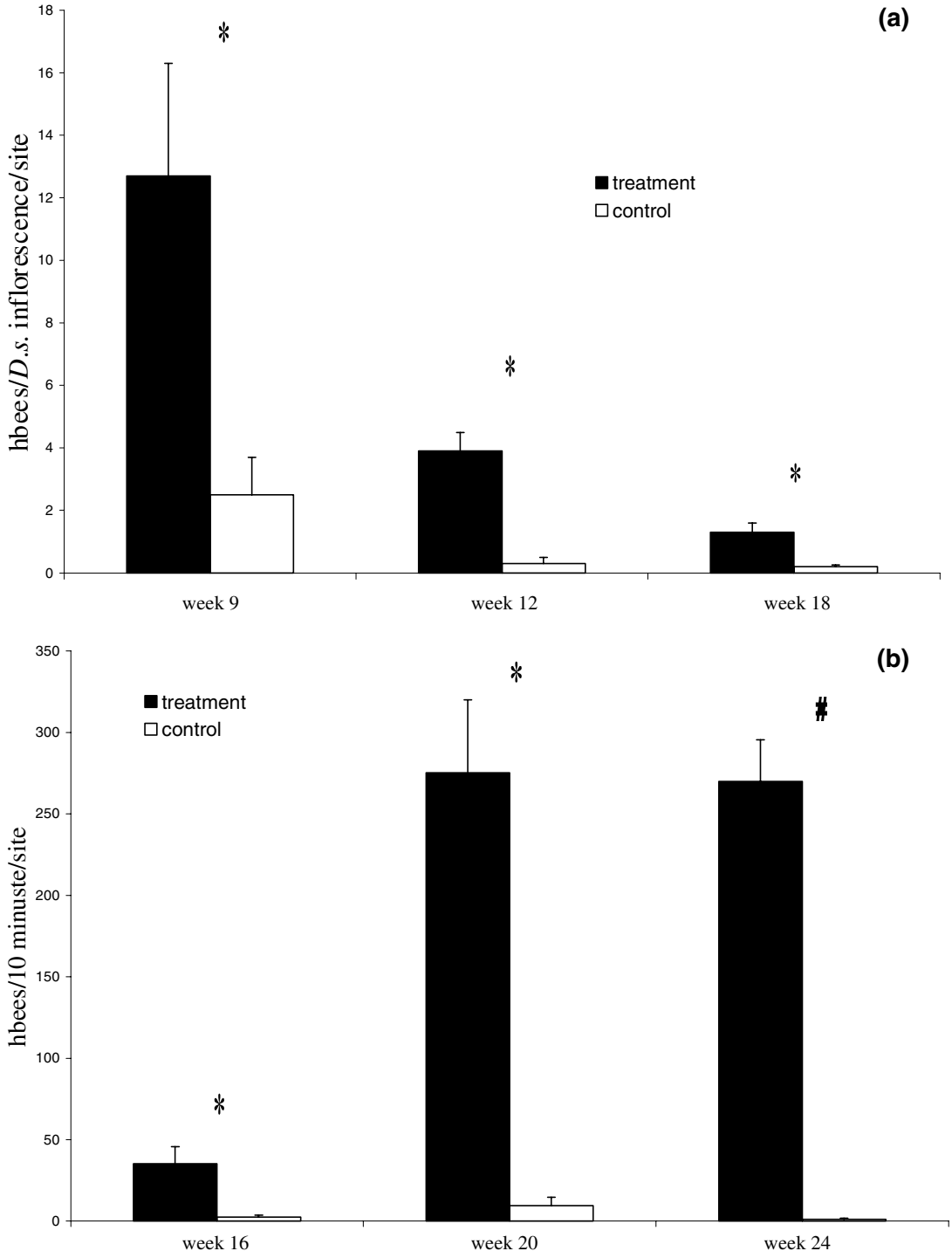


Fig. 2. Mean (+SE) honey bee densities at control and treatment sites for (a) 1999 and (b) 2000. *, $p < 0.05$; #, data failed Cochran's test for homogeneity, even after transformation so the ANOVA result could not be accepted (see Section 2.4).

### 3.4. Fecundity

In 1999, 30 *H. alcyoneus* nests were retrieved from all sites compared with 87 nests in 2000. Only three nests were retrieved from treatment sites for the entire 1999 experiment and it was not possible to make an assessment of *H. alcyoneus* fecundity in this season, apart from nest numbers.

#### 3.4.1. Nest numbers

Wilcoxon's sign-ranked test revealed a significant difference between treatment and control sites (*Wilcoxon*

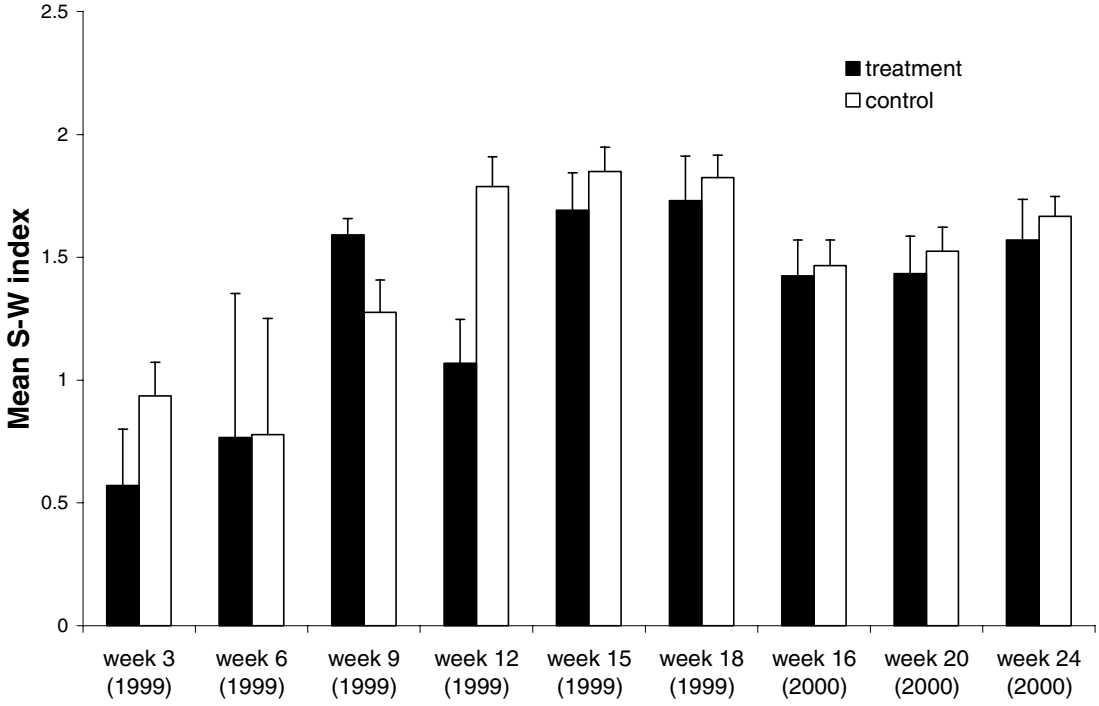


Fig. 3. Mean Shannon–Weiner index for flowering plant diversity from control and treatment sites (+SE). Week 12 '1999 was not significant after sequential Bonferroni adjustment.

Table 1
Mean resource overlap between *H. alcyoneus* and honey bees

| Week no. | Honey | Pollen |
|---|---|---|
| 1999 | | |
| 6 | –[a] | 0.72 |
| 9 | 0.61 | 0.52 |
| 12 | –[a] | 0.58 |
| 15 | 0.62 | 0.55 |
| 18 | 0.60 | 0.62 |
| 2000 | | |
| 8 | –[a] | –[b] |
| 12 | –[a] | –[b] |
| 16 | –[a] | 0.97 |
| 20 | 0.68 | 0.80 |
| 24 | 0.63 | 0.66 |

Pollen from *H. alcyoneus* nests was identified and compared to honey bee pollen and also pollen extracted from honey. Values vary between 0 and 1, with 0 equalling no overlap and 1 equalling 100% resource overlap.

[a] Frames not placed in hives or no honey was found in hive frames.

[b] Pollen samples lost due to mould.

$T_s = 5.5$, two-tailed test: $p < 0.05$, one-tailed test: $p < 0.025$). Of 11 measurement intervals over the course of two seasons, control sites produced more nests than treatment sites on 7 occasions (Fig. 4). The mean number of nests produced per measurement interval over both seasons was 23% less in treatment sites than control sites (treatment = 0.53 ± 0.20 SE; control = 0.85 ± 0.23 SE).

When analysed as separate measurement intervals using ANOVA, there were no significant differences in the number of completed *H. alcyoneus* nests between control and treatment sites for both 1999 and 2000 (Fig. 4), though power analysis revealed the experiment had low power ($p < 0.6$) to detect large differences between treatment and control even when $\alpha$ was set at 0.1.

### 3.4.2. Eggs per nest

In 2000, only one nest was retrieved from treatment sites in week 8 so ANOVA was not possible. Of the remaining weeks in 2000, no significant difference was detected between treatment and control sites (Fig. 5). Power analysis revealed that the experiment was only powerful enough ($p > 0.8$) to detect large differences (80–100%) between treatment and control sites (Table 2).

### 3.4.3. Emergent adult mass

As explained above, ANOVA was not possible for week 8, 2000 data. Of the remaining weeks in 2000, no significant difference was detected between treatment and control sites for mass of male or female adults emerging from nests (Fig. 6). Power analysis showed the experiment was powerful enough ($p > 0.8$) to detect at least a 50% difference between treatment and control sites when $\alpha$ was set at 0.1, with the exception of week 24 (Table 3). In one case (female mass, week 16) the experiment could detect a difference of 20% ($p = 0.96$).

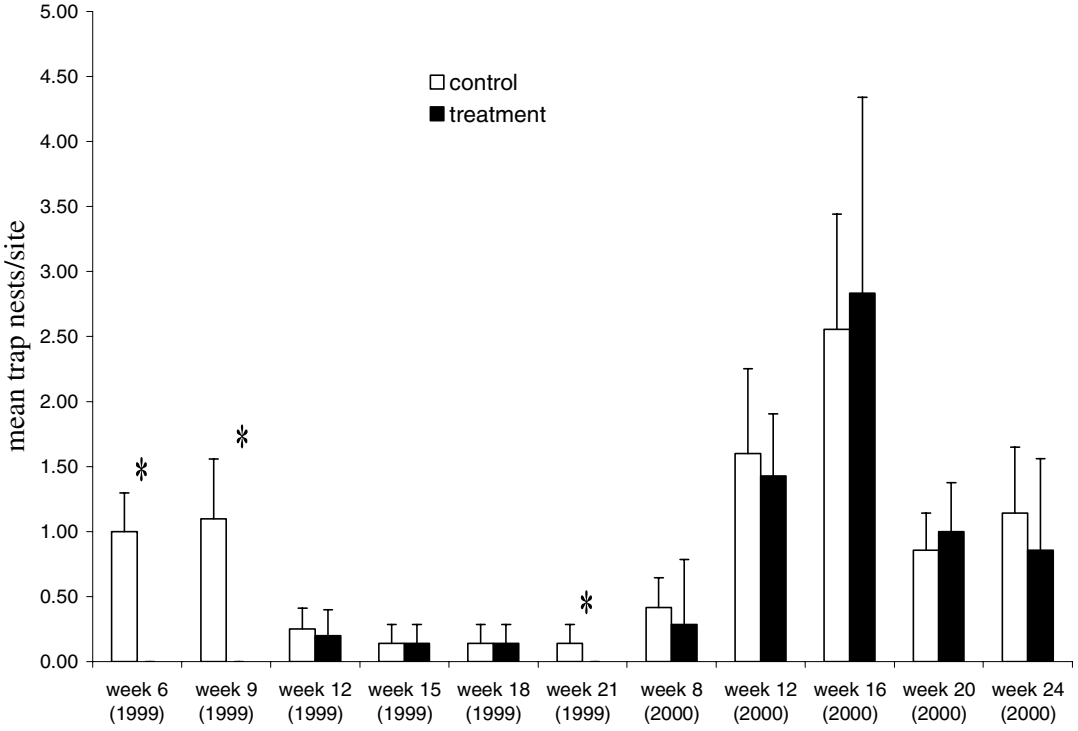


Fig. 4. Mean number of *H. alcyoneus* trap nests (+SE) throughout both seasons. In seven of 11 occasions more nests were recovered from control sites. *, a lack of variance in data, even after transformation, prevented ANOVA.

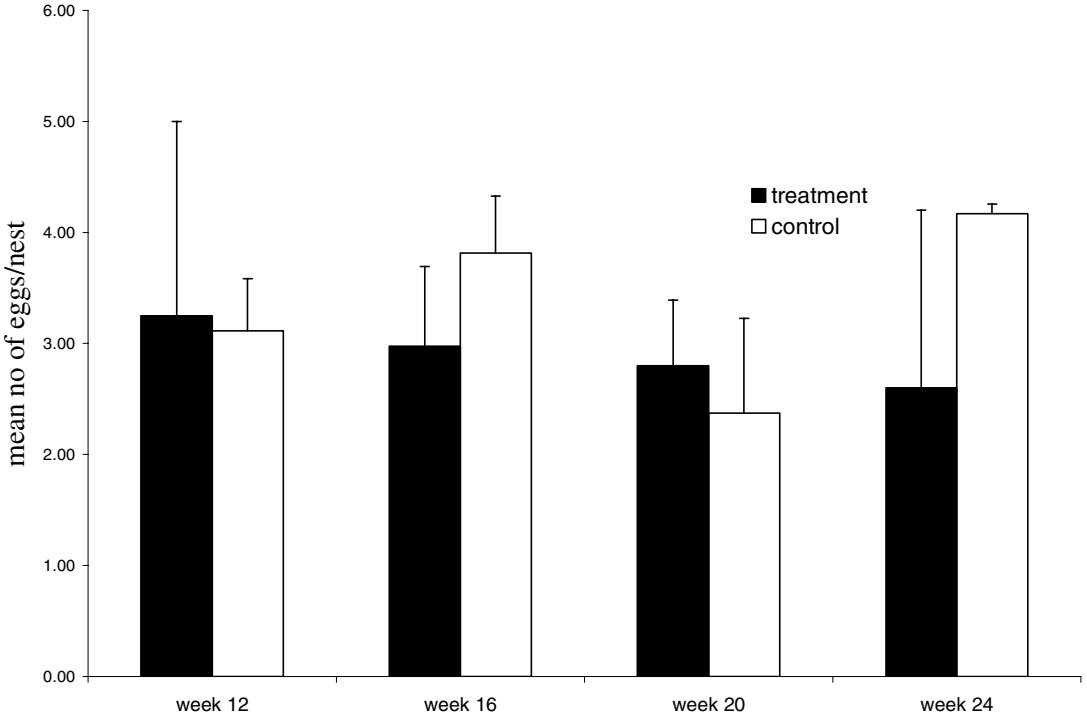


Fig. 5. The mean number of *H. alcyoneus* eggs per nest (+SE) in control and treatment sites in 2000.

Table 2
Power to detect differences of 20%, 50%, 80%, and 100% in the number of *H. alcyoneus* eggs/nest between control and treatment sites

| Week no | 20% | 50% | 80% | 100% |
|---|---|---|---|---|
| 12[a] | 0.08 | 0.23 | 0.49 | 0.67 |
| 12[b] | 0.14 | 0.35 | 0.64 | **0.81** |
| 16[a] | 0.12 | 0.46 | **0.85** | **0.96** |
| 16[b] | 0.20 | 0.61 | **0.93** | **0.99** |
| 20[a] | 0.07 | 0.18 | 0.38 | 0.54 |
| 20[b] | 0.13 | 0.29 | 0.54 | 0.70 |
| 24[c] | | | | |

[a] Power values when α was set at 0.05.
[b] Power values when α was set at 0.1.
[c] Data was heterogeneous, even after transformation so power analysis was not possible.

## 4. Discussion

### 4.1. Resource overlap

*Hylaeus alcyoneus* appears to be monolectic as *Banksia sphaerocarpa* was the only flowering plant species used to provision nests. Honey bees however, usually visited 4–5 different plant species, including *B. sphaerocarpa* for both nectar and pollen. Resource overlap between honey bees and *H. alcyoneus* ranged from 0.52 up to 0.97. There have been other studies reporting resource overlap between honey bees and native bees which have calculated values of resource overlap below 0.5 (Roubik, 1996; Wilms et al., 1996; Steffan-Dewenter

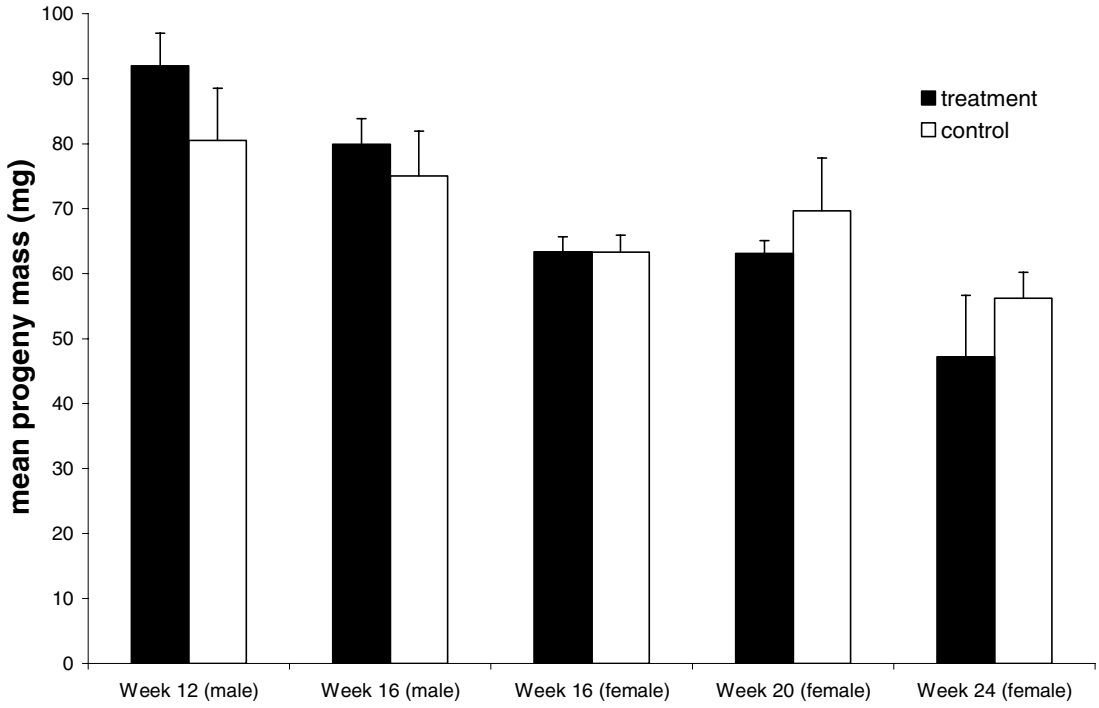


Fig. 6. The means mass (mg + SE) of emerging *H. alcyoneus* male and female progeny from nests of control and treatment sites in 2000. A lack of data for females from week 12, and males from weeks 20 and 24 prevented analysis.

Table 3
Power to detect differences of 20%, 50%, 80%, and 100% in the mass of *H. alcyoneus* male and female progeny in control and treatment sites

| Week no. | Sex | 20% | 50% | 80% | 100% |
|---|---|---|---|---|---|
| 12[a] | M | 0.16 | 0.65 | **0.96** | **1.00** |
| 12[b] | M | 0.26 | **0.80** | **0.99** | **1.00** |
| 16[a] | M | 0.30 | **0.95** | **1.00** | **1.00** |
| 16[b] | M | 0.44 | **0.98** | **1.00** | **1.00** |
| 16[a] | F | **0.90** | **1.00** | **1.00** | **1.00** |
| 16[b] | F | **0.96** | **1.00** | **1.00** | **1.00** |
| 20[a] | F | 0.17 | 0.67 | **0.90** | **1.00** |
| 20[b] | F | 0.30 | **0.85** | **0.98** | **1.00** |
| 24[a] | F | 0.15 | 0.58 | **0.91** | **1.00** |
| 24[b] | F | 0.26 | 0.77 | **0.98** | **1.00** |

[a] Power values when α was set at 0.05.
[b] Power values when α was set at 0.1.

and Tscharntke, 2000) though Wilms and Wiechers (1997) found values as high as 0.76 between honey bees and *Melipona bicolor* and *M. quadrifasciata* and Spessa (1999) found values between honey bees and *Amphylaeus morosus* varied from 0.16 to 0.86. Resource overlap between honey bees and *H. alcyoneus* therefore appears to be large, indicating the potential for competition between the two species.

Interestingly, *H. alcyoneus* only visited one plant species whether honey bees were present or not. If competition is occurring, *H. alcyoneus* may not be able to respond by using an alternative resource and honey bees may therefore represent a large threat to *H. alcyoneus* in this region.

### 4.2. Fecundity

*Hylaeus alcyoneus* constructed relatively few nests, though in 2000 almost three times as many nests were constructed as in 1999. Differences in resource levels between years or the unusually high rainfall may have caused the low number of nests in 1999. The total rainfall for May to August was 634.8 mm compared with the average of 449.4 mm (data provided by the Western Australian Bureau of Meteorology). Female *H. alcyoneus* will not forage during rain (personal observation DRP) and this reduction in foraging may have reduced the number of nests constructed in 1999. Environmental conditions may therefore have a large influence on population densities of this native bee.

Despite the large resource overlap reported here, analysing the measurement intervals separately did not reveal any impact of honey bees on *H. alcyoneus*. However, to determine the validity of any claim that honey bees had no impact, power analysis was conducted on these tests. This analysis was conducted setting $\alpha$ at the standard 0.05 and also at 0.10 as a number of researchers have argued for the relaxation of $\alpha$ in impact studies (Peterman, 1990a,b; Underwood, 1997; Calver et al., 1999). A relaxed $\alpha$ increases the chance of a type I error (claiming there is an impact when there is not) but this is preferable as it decreases the chance of a type II error (claiming there is not an impact when there is). A type II error may result in the loss of pollinator diversity, and the cost of reversing this damage may be too high (Fairweather, 1991). For many of the fecundity variables measured, power was poor except in male and female progeny mass which demonstrated good power ($p > 0.8$) over the entire second season. Progeny mass was therefore not affected by honey bees.

In determining the impact of honey bees on native bees, male and female progeny mass may be an important aspect of fecundity. Progeny mass is directly correlated with provision mass (Frohlich and Tepedino, 1986; Johnson, 1988) and for *H. alcyoneus*, progeny mass does decrease through the season as resources decrease (Paini and Bailey, 2002). If a bee species was experiencing competition from honey bees and there was less floral resource available, provision mass, and hence progeny mass, may be the first variable affected. For *H. alcyoneus* this variable showed no change in response to honey bees. However, females may compensate for a decreased resource by foraging longer. Longer foraging periods per progeny may result in a decrease in the number of nests produced and a Wilcoxon's sign test revealed that *H. alcyoneus* produced significantly less nests (23%) when honey bee were present.

Few studies in the world have shown that the reproductive output of a native bee species is negatively affected by honey bees (see Paini, 2004 for review). The reason for this lack of evidence may be that any impact may only be revealed over a long period. Clearly, experiments designed and conducted over longer periods are necessary to enable the detection of any subtle long-term impacts that may not be obvious from shorter studies.

Interestingly, despite the long-term agistment of honey bees in this area, an impact has been detected. A reasonable assumption would be that any impact would have been experienced long before and all that would be left was "the ghost of competition past". Clearly, this is not necessarily the case and competition can continue over a long period, perhaps fluctuating in intensity with each season depending on the environmental conditions and the various interactions within a complex ecosystem.

## Acknowledgements

This study was supported by funding from the Western Australian Department of Conservation and Land Management. We thank Win Bailey for reviewing this manuscript, Matt Williams for statistical advice, Terry Houston for native bee identifications, Lynne Milne for instruction in pollen preparation and identification, and beekeepers John Davies and Ron Pollard for their assistance and advice in conducting this study. The comments of two anonymous reviewers greatly improved this manuscript.

## References

Alcock, J., Houston, T.F., 1987. Resource defense and alternative mating tactics in the Banksia bee, *Hylaeus alcyoneus* (Erichson). Ethology 76, 177–188.

Allaby, M., 1994. The Concise Oxford Dictionary of Ecology. Oxford University Press, Oxford.

Butz Huryn, V.M., 1997. Ecological impacts of introduced honey bees. Quarterly Review of Biology 72, 275–297.

Calver, M.C., Bradley, J.S., Wright, I.W., 1999. Towards scientific contributions in applying the precautionary principle: an example

from southwestern Australia. Pacific Conservation Biology 5, 63–72.
Colwell, R.K., Futuyma, D.J., 1971. On the measurement of niche breadth and overlap. Ecology 52, 567–576.
Erdtman, G., 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Almquist and Wiksell, Stockholm.
Erdtman, H., 1960. The acetolysis method. A revised description. Svensk Botanisk Tidskrift 54, 561–564.
Fairweather, P.G., 1991. Statistical power and design requirements for environmental monitoring. Australian Journal of Marine and Freshwater Research 42, 555–567.
Faul, F., Erdfelder, E., 1992. GPOWER: A Priori, Post-hoc, and Compromise Power Analysis for MS-DOS. Bonn University, Department of Psychology, Bonn, FRG.
Frohlich, D.R., Tepedino, V.J., 1986. Sex ratio, parental investment, and interparent variability in nesting success in a solitary bee. Evolution 40, 142–151.
Gross, C.L., 1993. The breeding system and pollinators of *Melastoma affine* (Melastomataceae); a pioneer shrub in tropical Australia. Biotropica 25, 468–474.
Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6, 65–70.
Honek, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66, 483–492.
Houston, T.F., 1981. A revision of the Australian hylaeine bees (Hymenoptera: Colletidae). II. Australian Journal of Zoology 80, 1–128.
Johnson, M.D., 1988. The relationship of provision weight to adult weight and sex ratio in the solitary bee, *Ceratina calcarata*. Ecolgical Entomology 13, 165–170.
Magurran, A.E., 1988. Ecological Diversity and its Measurement. Croom Helm, London.
Oldroyd, B.P., Lawler, S.H., Crozier, R.H., 1994. Do feral honey bees (*Apis mellifera*) and regent parrots (*Polytelis anthopeplus*) compete for nest sites?. Australian Journal of Ecology 19, 444–450.
Paini, D.R., 2004. The Impact of the Introduced Honey Bee (*Apis mellifera*) (Hymenoptera: Apidae) on Native Bees: a review. Austral Ecology 29, 399–407.
Paini, D.R., Bailey, W.J., 2002. Seasonal sex ratio and unbalanced investment sex ratio in the Banksia bee *Hylaeus alcyoneus*. Ecological Entomology 27, 713–719.
Paton, D.C., 1996. Overview of the Feral and Managed Honeybees of Australia: Distribution, Abundance, Extent of Interactions with Native Biota, Evidence of Impacts and Future Research. Australian Nature Conservation Society.
Peterman, R.M., 1990a. Statistical power analysis can improve fisheries research and management. Canadian Journal of Fisheries and Aquatic Sciences 47, 2–15.
Peterman, R.M., 1990b. The importance of reporting statistical power: the forest decline and acidic deposition example. Ecology 71, 2024–2027.
Phipps, D., Playford, G., 1984. Laboratory Techniques for Extraction of Palynomorphs from Sediments. Papers, vol. 11. Department of Geology, University of Queensland, pp. 1–23.
Pyke, G., Balzer, L., 1985. The effects of the introduced honeybee (Apis mellifera) on Australian native bees. NSW National Parks and Wildlife Service Occasional Paper Number 7. NSW National Parks and Wildlife Service, Sydney.
Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43, 223–225.
Rodriguez, V.B., Riley, C., Shafron, W., Lindsay, R., 2003. Honeybee Industry Survey. Rural Industries Research and Development Corporation Publication No 03/039. Available from: http://www.rirdc.gov.au/reports/HBE/03-039.pdf.
Roubik, D.W., 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. Science 201, 1030–1032.
Roubik, D.W., 1983. Experimental community studies: time-series tests of competition between African and neotropical bees. Ecology 64, 971–978.
Roubik, D.W., 1996. Measuring the meaning of honey bees. In: Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P., Williams, H. (Eds.), The Conservation of Bees. Academic Press, London, pp. 163–172.
Schaffer, W.M., Zeh, D.W., Buchmann, S.L., Kleinhans, S., Schaffer, M.V., Antrim, J., 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64, 564–577.
Sokal, R.R., Rohlf, F.J., 1995. Biometry, third ed. Freeman, San Francisco.
Spessa, A., 1999. Behavioural and population ecology of an Australian native bee, *Amphylaeus morosus* (Colletidae: Hylaeinae). PhD, Australian National University, Canberra.
Steffan-Dewenter, I., Tscharntke, T., 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122, 288–296.
Sugden, E.A., Pyke, G.H., 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. Australian Journal of Ecology 16, 171–181.
Sugden, E.A., Thorp, R.W., Buchmann, S.L., 1996. Honey bee-native bee competition: focal point for environmental change and apicultural response in Australia. Bee World 77, 26–44.
Thomas, L., Krebs, C.J., 1997. A review of statistical power analysis software. Bulletin of the Ecological Society of America (April), 126–139.
Underwood, A.J., 1997. Environmental decision-making and the precautionary principle: what does this principle mean in environmental sampling practice?. Landscape and Urban Planning 37, 137–146.
Underwood, A.J., 1999. Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.
Underwood, A.J., Chapman, M.G., 2003. Power, precaution, type II error and sampling design in assessment of environmental impacts. Journal of Experimental Marine Biology and Ecology 296, 49–70.
Wenner, A.M., Thorp, R.W., 1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. In: Halvorson, W.L., Maender, G.J. (Eds.), The Fourth California Islands Symposium: Update on the Status of Resources. Santa Barbara Museum of Natural History, Santa Barbara, pp. 513–522.
Williams, M.R., Abbott, I., Liddelow, G.L., Vellios, C., Wheeler, I.B., Mellican, A.E., 2001. Recovery of bird populations after clearfelling of tall open eucalypt forest in Western Australia. Journal of Applied Ecology 38, 910–920.
Wills, R.T., Lyons, M.N., Bell, D.T., 1990. The European honey bee in Western Australian kwongan: foraging preferences and some implications for management. Proceedings of the Ecological Society of Australia 16, 167–176.
Wilms, W., Imperatriz-Fonseca, V.L., Engels, W., 1996. Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honey bee on native stingless bees in the Brazilian Atlantic rainforest. Studies on Neotropical Fauna and Environment 31, 137–151.
Wilms, W., Wiechers, B., 1997. Floral resource partitioning between native Melipona bees and the introduced Africanized honey bee in the Brazilian Atlantic rain forest. Apidologie 28, 339–355.