

Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: A review

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Abstract Interspecific competition for a limited resource can result in the reduction of survival, growth and/or reproduction in one of the species involved. The introduced honey bee (*Apis mellifera* Linnaeus) is an example of a species that can compete with native bees for floral resources. Often, research into honey bee/native bee competition has focused on floral resource overlap, visitation rates or resource harvesting, and any negative interaction has been interpreted as a negative impact. Although this research can be valuable in indicating the potential for competition between honey bees and native bees, to determine if the long-term survival of a native bee species is threatened, fecundity, survival or population density needs to be assessed. The present review evaluates research that has investigated all these measurements of honey bee/native bee competition and finds that many studies have problems with sample size, confounding factors or data interpretation. Guidelines for future research include increasing replication and using long-term studies to investigate the impact of both commercial and feral honey bees.

Key words: competition, honey bee, native bee, resource.

INTRODUCTION

Begon *et al.* (1990) defined competition between organisms as 'an interaction between individuals, brought about by a shared requirement for a resource that is in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the competing individuals concerned'. In this way, the active or passive introduction of organisms to new countries and continents has generally reinforced the classical view of Gause that two or more species with the same ecologies cannot exist in the same environment (Gause 1934 cited in Putman & Wratten 1984). Although many introductions have been accidental, others have been deliberate, and a result of changing human culture and farming practice. Such introductions can result in competition between native and introduced organisms (Miller & Aplet 1993).

Australia has a long history of species introduction, often as a result of poor quarantine but more significantly in a desire to Europeanize the continent (Flannery 1994). Rabbits (*Oryctolagus cuniculus*) were first introduced to Australia in 1788 and have been found to compete with the red kangaroo (*Macropus rufus*; Dawson & Ellis 1994), rock-wallabies (*Petrogale* spp.; Pearson & Kinnear 1997) and the rufous hare-wallaby (*Lagorchestes hirsutus*; Lundie-Jenkins *et al.* 1993). Similarly, the pig (*Sus scrofa*) excludes the

endangered northern bettong (*Bettongia tropica*) from areas in tropical Queensland (Laurance 1997).

Exotic insects, like the tramp ant (*Pheidole megacephala*), the bumble bee (*Bombus terrestris*) and the European honey bee (*Apis mellifera*), can also show competitive interactions with Australian native insects. *P. megacephala* reduces native ant abundance and richness (Majer 1985; Hoffmann *et al.* 1999), while *B. terrestris* displaces two native bee species from floral resources in Tasmania (Hingston & McQuillan 1999). The honey bee was introduced during the nineteenth century for honey production (Thorp 1987). It was not until the late 1970s, however, that honey bees were first viewed as an invasive species that might not be pollinating native flowering plants and might also be out-competing native fauna for nectar and pollen (Paton 1996). Although competition from honey bees can affect all nectar-feeding animals, native bees are the logical focus for any investigation. Like honey bees, native bees rely on nectar and pollen for nutrition and for their brood. In addition, native bees are the most dominant pollinators in natural ecosystems and thus are vital to the maintenance of biological diversity (Sugden *et al.* 1996).

Worldwide, most research to date into honey bee/native bee competition has concentrated on one or more of the following three measurements: the overlap in resource use between honey bees and native bees; the change in visitation rates of native bees; and the change in the levels of resource harvested by native bees when honey bees are present (Table 1). The implication of any measurable changes in the above three aspects has been that the presence of honey bees will impact on the

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fecundity or adult survival of native bees and, ultimately, their population density (Paton 1996). However, such conclusions might not be justified.

For competition to occur between honey bees and native bees, there must first be an overlap of floral

resource, with both species collecting nectar and pollen from the same flower species (Fig. 1). Although both species might visit flowers, competition can be absent if the presence of honey bees fails to interfere with native bee visitation rates or if floral resources are not

Table 1. Studies investigating the impact of honey bees on native bees, grouped into the measurements employed to determine impact

Country	Study animal	Sites	Impact [†]	Reviewed paper [‡]	Author(s)
Resource overlap					
Germany	Solitary Apoidea	2	0	Y	Fotler (1995)
Ogasawara Islands	Colletidae, Megachilidae, Anthophoridae	7	–	Y	Kato (1992)
Ogasawara Islands	Colletidae, Megachilidae, Anthophoridae	7	–	Y	Kato <i>et al.</i> (1999)
Brazil	Native bees	1	0	Y	Pedro and Camargo (1991)
Brazil	Native bees	1	–	Y	Wilms <i>et al.</i> (1996)
Australia	Native bees	90	–	Y	Wills <i>et al.</i> (1990)
Visitation rates					
Argentina	Native insects	4	0	Y	Aizen and Feinsinger (1994)
USA	Native bees	1	–	Y	Ginsberg (1983)
New Zealand	Native insects	4	–	Y	Murphy and Robertson (2000)
USA	<i>Bombus bifarius</i> and <i>Bombus flavifrons</i>	2	–	Y	Pleasants (1981)
French Guiana	<i>Melipona</i> spp.	1	–	Y	Roubik (1978)
French Guiana	<i>Melipona fulva</i> , <i>Trigona</i> spp.	9	–	Y	Roubik (1980)
Costa Rica	<i>Trigona corvina</i>	1	–	Y	Roubik (1981)
French Guiana	<i>Melipona</i> spp.	1	0	Y	Roubik (1996)
Japan	<i>Apis cerana</i>	1	–	Y	Sakagami (1959)
USA	<i>Bombus sonorus</i> and <i>Xylocopa arizonensis</i>	6	–	Y	Schaffer <i>et al.</i> (1979)
USA	<i>Bombus sonorus</i> and <i>Xylocopa arizonensis</i>	1	–	Y	Schaffer <i>et al.</i> (1983)
USA	Native bees	2	–	N	Wenner and Thorp (1994)
New Zealand	<i>Bombus terrestris</i> , <i>Bombus ruderatus</i>	1	–	Y	Wratt (1968)
Australia	<i>Nomia</i> sp.	1	–	N	Bailey (1994)
Australia	Native bees	1	–	Y	Gross and Mackay (1998)
Australia	Native bees	2	0	Y	Gross (2001)
Australia	Native insects	2	0	Y	Horskins and Turner (1999)
Australia	Native insects	15	0	N	Paton (1999)
Australia	Native bees	1	–	N	Pyke and Balzer (1985)
Resource harvesting					
Brazil	<i>Melipona bicolor</i> and <i>Melipona quadrifasciata</i>	1	–	Y	Wilms and Wiechers (1997)
Panama	<i>Melipona</i> spp., <i>Trigona</i> spp.	1	–	Y	Roubik <i>et al.</i> (1986)
India	<i>Apis indica</i>	?	–	N	Atwal and Sharma (1971)
Adult survival					
USA	<i>Bombus sonorus</i> and <i>Xylocopa californica</i>	1	–	Y	Thoenes (1993)
Fecundity					
Germany	<i>Megachile rotundata</i>	2	–	Y	Evertz (1995)
Austria	Native bees	1	0	Y	Pechhacker and Zeillinger (1994)
French Guiana	<i>Melipona favosa</i> and <i>Melipona fulva</i>	2	0	Y	Roubik (1983)
Germany	Native bees	15	0	Y	Steffan-Dewenter and Tschardt (2000)
Australia	<i>Exoneura bicolor</i> and <i>Exoneura nigrihirta</i>	6–8	0/+	N	Schwarz <i>et al.</i> (1991, 1992a,b)
Australia	<i>Amphylaeus morosus</i>	8	0/+	N	Spessa (1999)
Australia	<i>Exoneura asimillima</i>	4	–	Y	Sugden and Pyke (1991)
Population density					
Panama	Native bees	1	0	Y	Roubik and Wolda (2001)

[†]Conclusion of the author(s) as to the impact of honey bees on native bees; [‡]there is considerable information in theses and reports that are listed here as unreviewed papers. –, negative impact; +, positive impact; ?, Authors did not indicate the number of sites used; 0, no impact; N, not reviewed; Y, reviewed.

limiting. Visitation rate and the level of resource harvesting of native bees will, under these conditions, remain unchanged. Even if native bees are experiencing competition from honey bees, they might not be able to change visitation rates in response and the amount of resource harvested will be reduced (Fig. 1). Alternatively, the presence of honey bees visiting the same floral resources might cause a decrease in native bee visitation rates. However, as with floral resource overlap, reduced visitation rates of native bees might not necessarily equate to a negative impact. If native bees compensate for reduced visitation rates – for example by foraging longer through the day – their level of resource harvesting could remain unchanged (Fig. 1). Furthermore, if reduced visitation rates of native bees result in a decrease in harvested resource,

native bees might use an alternative floral species. If this alternative floral resource provides nectar and pollen in the same quantity and quality at no cost to survival or fecundity, then, although there might be evidence of competition for one resource, there might be no evidence of a negative impact on native bees (Fig. 1).

Competition can be defined as a negative interaction between populations (Grover 1997) and therefore any interaction that simply changes the behaviour of native bees can be defined as competition and subsequently a negative impact. This review defines a negative impact as that which reduces individual fitness and therefore threatens the long-term survival of a population. Under this more specific definition a change in behaviour, such as reduced visitation rate or switching to an alternative resource, might not lead to a negative

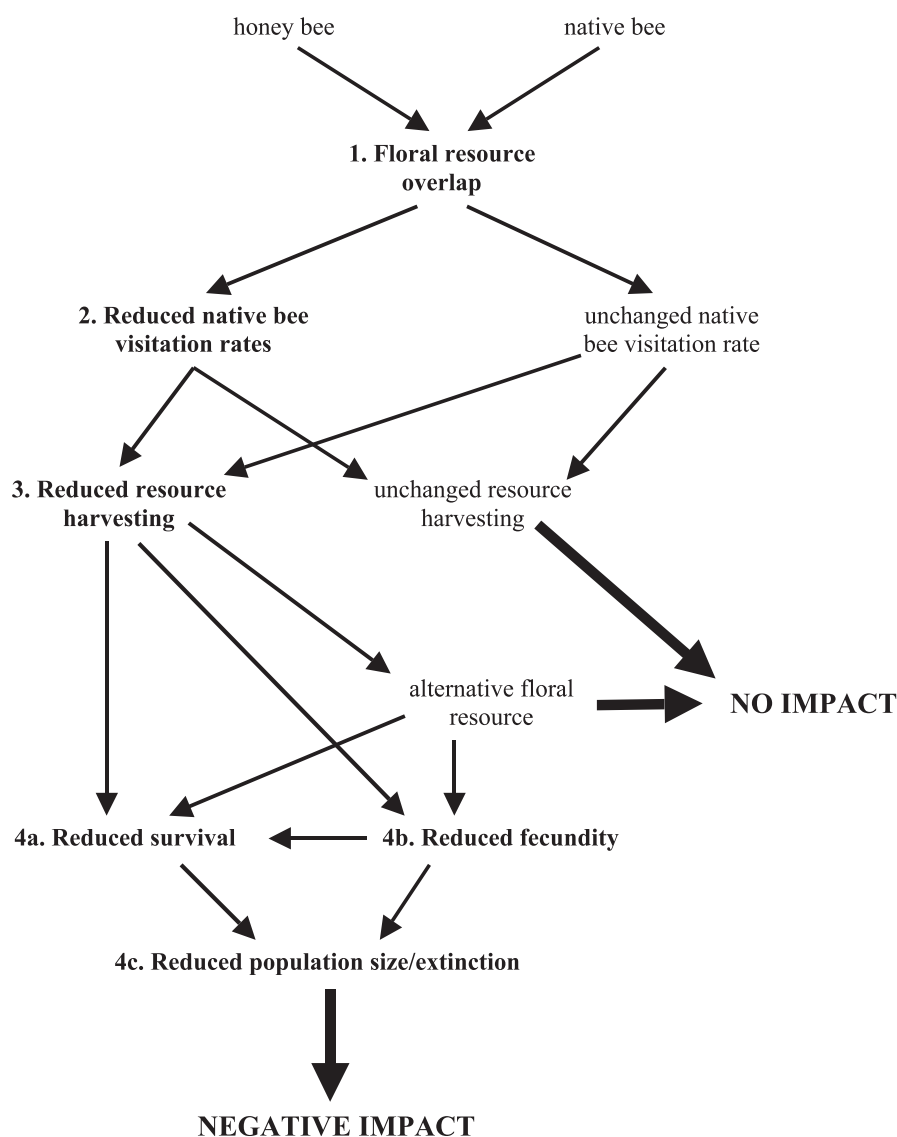


Fig. 1. To determine if competition is occurring between honey bees and native bees, researchers have assessed a number of measurements (1–3, 4a–c). However, measurements 1–3 can result in either no impact or a negative impact on native bees. Only measurements 4a–c will definitely lead to a negative impact on native bees.

impact on the species directly competing with honey bees. Furthermore, any change in native bee behaviour can have implications for the ecosystem it occupies. A native bee that switches from one plant species to another in response to the presence of honey bees might influence pollination of both the new and old plant species, or create a situation where other native pollinators now compete with the native bee species. But although second and third order impacts of this nature can occur, they have never been documented in studies of honey bee/native bee competition.

Clearly, the three measurements by which competition between honey bees and native bees can be assessed (floral resource overlap, visitation rates and resource harvesting) are indirect and might not result in a negative impact on native bees. Only by assessing direct measurements such as individual survival, fecundity or population numbers can a negative impact be determined (Fig. 1). Nevertheless, studies investigating these indirect measurements of competition are valuable, as they indicate the potential for competition between honey bees and native bees. This review evaluates research on all measurements in which competition between honey bees and native bees has been assessed. In the first section, studies of the three indirect measurements mentioned above are assessed, initially focusing on the problems associated with these studies (replication, confounding factors and data interpretation) before discussing the results of the remaining studies. The second section assesses the few studies that have used direct measurements (individual survival, fecundity or population numbers) for determining honey bee/native bee competition.

INDIRECT MEASUREMENTS: RESOURCE OVERLAP, VISITATION RATES AND RESOURCE HARVESTING

I reviewed 28 studies investigating interactions between honey bees and native bees using indirect measurements.

Replication

One of the common flaws in studies investigating the impact of honey bees on native bees has been lack of replication of sites, with 19 studies (68% of 28 studies) using two sites or fewer (Table 1). For example, Pedro and Camargo (1991) collected bees visiting flowers from 140 plant species over a 1-year period in a natural 'cerrado' ecosystem in Brazil. Honey bee floral preference overlapped with that of native bees, particularly those belonging to the Meliponinae, but sampling occurred at only one site. In the USA, Ginsberg (1983), using information from only one

site, found that honey bees foraged on large flower clusters and native bees foraged on small flower clusters. Finally, Bailey (1994) reported an increase in native bee densities when honey bees were prevented from visiting one flowering bush of *Leucopogon propinquus* over a series of days.

Confounding factors

Confounding factors compromised the interpretation of results in three (11%) of the 28 studies. Wratt (1968) compared the visitation rates of two species of bumblebees (*B. terrestris* and *Bombus ruderatus*) with those of honey bees on red clover (*Trifolium pratense*). As temperature increased, the number of *B. ruderatus* decreased and the number of honey bees increased. Wratt (1968) concluded that competition was occurring between honey bees and *B. ruderatus*. However, an alternative hypothesis, not considered in this study, is that temperature was the factor causing changes in visitation rates. On the Bonin (Ogasawara) Islands in the Pacific Ocean, Kato (1992) and Kato *et al.* (1999) demonstrated an overlap in resource use between honey bees and a number of native bees including colletids, megachilids and anthophorids. These authors argued that native bee species had disappeared from two of the islands because of the presence of honey bees. However, the islands have also undergone major habitat destruction and invasion by exotic plants as a result of human activity, and it is equally possible that these factors, rather than honey bees, resulted in a reduction in native bee biodiversity.

Interpretation of results

Pyke and Balzer (1985) investigated visitation rates of native bees in response to honey bees in four experiments and found conflicting results. In the first experiment, when honey bees were removed from sites, the number of native bees visiting these sites appeared to increase significantly. In the second experiment, a census area was surveyed at three distances from an established apiary. The authors expected honey bee density to decrease with distance from hives and native bee density to increase, but both honey bee and native bee density increased with distance. In the third experiment, 30 hives were added to a site and honey bees, counted from transects, increased at all plots except the furthest one from the hives (1000 m). Native bee density decreased at all plots except the furthest suggesting a negative impact. However, although honey bee visitation rates to flowering *Prostanthera cuneata* (its only nectar source) generally increased when honey bee hives were added, native bee visitations did not decrease significantly.

A fourth experiment showed no significant negative relationship between densities of honey bees and native bees on any flowering species. In fact, for *Angophora hispida*, as honey bee density increased so did native bee densities. Despite the contradictory results of the four experiments, the authors concluded that native bees were excluded from or avoided areas of high honey bee densities. Overall, only the first experiment provides any supporting evidence that honey bees negatively impact on native bees, whereas the remaining experiments remain ambiguous.

In four studies (14% of studies), the authors recognized the shortcomings of their work and reached few conclusions for a number of reasons. Wilms *et al.* (1996) calculated the degree of resource overlap for 17 species of native stingless bees and honey bees in Brazil. They found honey bees overlapped more with other stingless bees than stingless bees did with each other, and concluded that stingless bees suffer more competitive pressure from the honey bee than from each other. However, no conclusions were made regarding the possible decline of stingless bees as a result of this competition. In fact, the authors argued that stingless bees should be able to avoid competition with honey bees as the mass flowering conditions that occur during the period in which the experiment was conducted would probably prevent depletion of nectar resources.

Again in South America, honey bees were found to be more common than native bees in small patches of subtropical forest in Argentina, whereas native bees were more common than honey bees in large patches (Aizen & Feinsinger 1994). This result could have been interpreted as evidence for the competitive exclusion of native bees by honey bees, but the complicating factor of patch size prevented the authors from drawing any conclusions.

In an Australian study, 70% of the plants visited by honey bees were also visited by native bees (Wills *et al.* 1990) and a potential for competition between honey bees and native bees was considered, but again no conclusions were drawn from this study. Gross (2001) found that visitation rates of honey bees and native bees on *Dillwynia juniperina* were negatively related and this implied a negative impact of honey bees on native bees. However, the author indicated no conclusion could be made without examining brood levels in response to honey bee competition.

Interference competition

When visitation rates are measured, not only exploitative competition can occur but also interference competition, with honey bees displacing native bees from floral resources by their physical presence. For example, in Japan, Sakagami (1959) found that at

an artificial nectar source, *A. mellifera* and *Apis cerana* attacked each other and eventually *A. cerana* were excluded. Roubik (1980) also reported low levels of honey bee aggression toward both meliponine and polybiine wasps at artificial feeders, although he pointed out that aggressive interactions are much more likely at such feeders as they provide unusually rewarding resources. In Australia, Gross and Mackay (1998) found that in 91% of honey bee/native bee interactions on *Melastoma affine*, native bee foraging was disrupted by honey bees. They also observed honey bees grappling with native bees in an attempt to pull them off flowers.

No impact

Finally, three of the 28 studies (11%) failed to find any impact on native bee visitation rates in response to honey bees. Roubik (1996) followed up an investigation from 17 years earlier (Roubik 1978) in which he had predicted that competition from honey bees might lead to a population decline in native pollinators. There was no evidence for local extinction or population decline of native *Melipona* spp. resulting from honey bee competition. In an Australian study, Paton (1999) found no impact of honey bees on visitation rates of native pollinating insects, and Horskins and Turner (1999) showed that honey bees rarely depleted nectar resources completely.

DIRECT MEASUREMENTS: SURVIVAL, FECUNDITY AND POPULATION DENSITY

I located nine studies that investigated competition by direct measurements such as native bee fecundity, survival or population density (Table 1). Three were conducted in Europe (Pechhacker & Zeillinger 1994; Evertz 1995; Steffan-Dewenter & Tschardt 2000). Evertz (1995) found the reproductive success of *Megachile rotundata* was higher in a site without honey bees than in one with honey bees, but the study lacked site replication, and other factors could have been involved. The other two European studies found no impact of honey bees on native bees (Pechhacker & Zeillinger 1994; Steffan-Dewenter & Tschardt 2000). This is not surprising as honey bees are native to Europe and are likely to have evolved with other native bees to reduce niche overlap and limit competition.

By comparison, in French Guiana, Roubik (1983) introduced colonies of native bees (*Melipona favosa* and *Melipona fulva*) to two sites then added honey bees for 30 days. There was no evidence of decreased fecundity or resource harvesting of the two *Melipona* spp. while the honey bees were present. In Panama, Roubik and

Wolda (2001) recorded bee species caught in two light traps for 7 years before honey bees invaded and 10 years following invasion. There was no evidence of a decrease in the relative population levels of 15 of the most common bee species. Thoenes (1993) found that honey bee hives in the USA attracted native bee species, which were then attacked and killed by the honey bees, suggesting local populations of native bees could be impacted. As with many other papers researching honey bee/native bee competition, the three studies above lack replication (two sites, one site and one site, respectively).

The remaining studies in Table 1 were conducted in Australia. Sugden and Pyke (1991) found that honey bees and *Exoneura asimillima*, a native, semisocial bee in New South Wales, overlapped in their use of nectar and pollen from a wide range of plants. Fewer adult *E. asimillima* were found in established nests at one site with honey bees present than at three sites where they were absent. This was attributed to higher migration or death rates. Additionally, founder nests (newly formed colonies) at the site with honey bees contained more adult females, pupae and eggs. The authors suggested adults were being forced out of established nests because resources were depleted by honey bees. However, Paton (1996) argued that higher numbers of newly formed nests in the presence of honey bees could indicate greater native bee fecundity. But the authors acknowledged that unmeasured aspects of microclimate might have varied between sites with and without honey bees and, without adequate replication, their conclusions were tentative.

Schwarz *et al.* (1991, 1992a,b) found no negative impact of either commercial or feral honey bees on *Exoneura bicolor* and *Exoneura nigrihirta* in terms of brood mass, brood number and adult number. Native bee colonies had higher survival at sites where honey bees were present, perhaps because high honey bee numbers can saturate a predator population and reduce predation on native bees.

Spessa (1999) investigated the impact of honey bees on a native colletid bee (*Amphylaeus morosus*) at eight sites over two seasons, reversing the control and impact sites between seasons to control for site effects. Although resource overlap between honey bees and *A. morosus* averaged 52%, no negative impact of honey bee presence could be detected, and in one season there were more new nests of the native bee in the presence of honey bees. Spessa (1999) concluded that nectar and pollen are not limiting for *A. morosus*.

CONCLUSION

Although previous studies investigating indirect measurements have been cited as evidence of competition between honey bees and native bees (Matthews

1984; Hopper 1987; Pyke 1990), many of these studies were compromised by low replication, confounding factors or poor interpretation. Studies that are well designed and implemented might conclude that honey bees have the *potential* to impact negatively on native bees but the use of indirect measurements does not reveal long-term survival of native bees.

More direct studies of the impact of honey bees on native bee survival, fecundity or population density have shown little evidence that the presence of honey bees has any impact on native bees (Butz Huryn 1997). However, in the present review only nine studies were found worldwide that focused on these three aspects of honey bee/native bee competition and it is therefore inadvisable to make any definite conclusion until more research is conducted.

Any future research should investigate the impact of both commercial and feral honey bees. In Australia, beekeepers rotate their commercial honey bee hives from one area of native vegetation to another. Often, hive agistment is opportunistic, with many locations experiencing a good flowering season only once every 2 or 3 years. Although honey bee agistment is usually short-term (1–3 months), the number of honey bees involved (up to 100 hives at each site) can potentially have a large impact on native pollinators. Additionally, feral honey bees, present in the same location throughout the year, can have a large impact on native bees when floral resources are low.

In Australia, honey bees have been present in many areas for decades, particularly in those sites used for commercial honey bees, and native bee species vulnerable to honey bee competition might have already disappeared. However, to disregard these areas as 'lost causes' would not only remove the majority of native vegetation around Australia from study, but also deny the possibility that competition could still be occurring. Clearly, not only should untouched areas be investigated but also those areas that have experienced the long-term presence of honey bees.

One difficulty in demanding further study is the question of how many studies are enough. Australia has a variety of climates, ecosystems and bee assemblages and there might be no simple, single response to honey bees across these ecosystems. It could therefore be more appropriate to focus on areas of high interest or conservation. This might include targeting native bee species that are more likely to be sensitive to honey bee competition such as short tongued bees or monolectic bees (Schwarz & Hurst 1997). However, high levels of variation in native bee diversity and density over space and time can make evaluating the impact on many native bee species difficult (Williams *et al.* 2001b). Although increasing sites and duration of experiments could enable assessment of the impact on common, widespread bee species, the impact on rare species might remain unknown (Williams *et al.* 2001b). In

focusing on common native bee species, researchers should consider using 'before–after, control–impact' studies, which compare differences between control and impact sites before an impact is introduced to any differences after (Stewart-Oaten *et al.* 1986). Researchers might also need to consider relaxing alpha (Peterman 1990a,b; Underwood 1997; Calver *et al.* 1999). Although this increases the chance of a Type I error (claiming there is an impact where there is none) it decreases the chance of a Type II error (claiming there is not an impact where there is one). Finally, post-hoc power analysis should be performed on any experiments that do not reveal a significant result. An experiment with adequate power ($P > 0.8$; Williams *et al.* 2001a) at an ecologically meaningful effect size would give researchers greater confidence in claiming no impact.

Despite the paucity of research investigating the question of honey bee/native bee competition, the first steps have been taken. Researchers have started to realize the importance of assessing direct measurements. Indirect measurements can assess rapidly the potential for competition, but direct measurements are needed to confirm competition. A more focused approach using experiments with increased replication and over several seasons (Sugden *et al.* 1996) could give the answers that are currently required.

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