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EFFECTS OF INTRODUCED BEES ON NATIVE ECOSYSTEMS

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■ **Abstract** Bees are generally regarded as beneficial insects for their role in pollination, and in the case of the honeybee *Apis mellifera*, for production of honey. As a result several bee species have been introduced to countries far beyond their home range, including *A. mellifera*, bumblebees (*Bombus* sp.), the alfalfa leafcutter bee *Megachile rotundata*, and various other solitary species. Possible negative consequences of these introductions include: competition with native pollinators for floral resources; competition for nest sites; co-introduction of natural enemies, particularly pathogens that may infect native organisms; pollination of exotic weeds; and disruption of pollination of native plants. For most exotic bee species little or nothing is known of these possible effects. Research to date has focused mainly on *A. mellifera*, and has largely been concerned with detecting competition with native flower visitors. Considerable circumstantial evidence has accrued that competition does occur, but no experiment has clearly demonstrated long-term reductions in populations of native organisms. Most researchers agree that this probably reflects the difficulty of carrying out convincing studies of competition between such mobile organisms, rather than a genuine absence of competitive effects. Effects on seed set of exotic weeds are easier to demonstrate. Exotic bees often exhibit marked preferences for visiting flowers of exotic plants. For example, in Australia and New Zealand many weeds from Europe are now visited by European honeybees and bumblebees. Introduced bees are primary pollinators of a number of serious weeds. Negative impacts of exotic bees need to be carefully assessed before further introductions are carried out.

INTRODUCTION

The devastating impacts that some exotic organisms have wreaked on native ecosystems surely ought to have taught us a lesson as to the perils of allowing release of alien species. The introduction of Nile perch to Lake Victoria, and of cane toads, prickly pear, rabbits, foxes, and cats among numerous others to Australia, are perhaps some of the best known examples, but they constitute only the tip of the iceberg. Australia alone had 24 introduced mammal species, 26 birds, 6 reptiles, 1 amphibian, 31 fish, more than 200 known invertebrates, and no less than 2,700 non-native plants at the last count (Alexander 1996; reviewed in Low 1999). A strong case can be made that exotic species represent the biggest threat to global biodiversity after habitat loss (Pimm et al. 1995, Low 1999).

Whereas the threat posed by exotic species is now widely appreciated, exotic bees appear to have received disproportionately little attention. Bees are widely perceived to be beneficial, for their role in the pollination of crops and wildflowers and, in the case of the honeybee *Apis mellifera* (L.) (Apidae), for the production of honey. Because of these economic benefits there is reluctance to regard bees as potentially damaging to the environment. As long ago as 1872, Darwin stated that honeybees in Australia were "rapidly exterminating the small, stingless native bee." In fact the bee he refers to, presumably *Trigona carbonaria* Sm., is still abundant. However, almost no research was carried out upon the impact of honeybees until the 1980s, by which time they had long since become established on every continent except Antarctica.

Here I review the scale on which bees have been artificially distributed around the globe. Three bee species, the honeybee *A. mellifera*, the bumblebee *Bombus terrestris* (L.) (Apidae), and the alfalfa leaf-cutter bee *Megachile rotundata* (Fabr.), are of particular concern because their range has been considerably expanded owing to both deliberate and accidental releases. I examine the potential consequences of this range expansion.

The possible undesirable effects of exotic bees include:

1. Competition with native flower visitors for floral resources;
2. Competition with native organisms for nest sites;
3. Transmission of parasites or pathogens to native organisms;
4. Changes in seed set of native plants (either increases or decreases);
5. Pollination of exotic weeds.

I examine evidence for each of these processes in turn. Reviewing studies to date serves to highlight the substantial gaps in our knowledge. I suggest further experimental approaches that may provide less equivocal answers as to the threat posed by these exotic organisms.

DISTRIBUTION AND ABUNDANCE OF INTRODUCED BEES

The honeybee is thought to be native to Africa, western Asia, and southeast Europe (Michener 1974), although its association with man is so ancient that it is hard to be certain of its origins. It has certainly been domesticated for at least 4000 years (Crane 1990a), and has been introduced to almost every country in the world. It is now among the most widespread and abundant insects on earth. The European strain of the honeybee appears to be adapted to temperate and Mediterranean climates, and flourishing feral populations occur throughout much of Asia, North America, the southern half of South America, and Australia. Major events in this range expansion include its introduction to North America in about 1620 (Buchmann & Nabhan 1996), to Australia in 1826 (Doull 1973), and to New Zealand in 1839 (Hopkins 1911). The African race, *A. mellifera scutellata* Lepeletier, is associated with tropical forests and savannas, and has spread throughout the neotropics and into North America following its introduction to Brazil in 1957.

More recently, bumblebees (*Bombus* spp.), a group whose natural range is largely confined to the temperate northern hemisphere, have been introduced to various countries to enhance crop pollination. New Zealand has four established *Bombus* species native to the U.K., *B. hortorum* (L.), *B. terrestris*, *B. subterraneus* (L.), and *B. ruderatus* (F.), following introductions in 1885 and 1906 intended to improve pollination of red clover, *Trifolium repens* (Hopkins 1914). *B. hortorum* and *B. subterraneus* have restricted distributions within New Zealand, whereas *B. terrestris* and *B. ruderatus* have become ubiquitous (Macfarlane & Gurr 1995). *B. terrestris* spread into Israel in the 1960s (Dafni & Shmida 1996), perhaps as a result of the presence of introduced weeds. This species has also become established in the wild in Japan following escapes from commercial colonies used for pollination in glass houses (Dafni 1998). Most recently, *B. terrestris* arrived in Hobart, Tasmania, in 1992, perhaps accidentally transported in cargo, and has since spread out to occupy a substantial portion of the island (Buttermore 1997, Stout & Goulson 2000, Hingston et al. 2002). *B. ruderatus* was introduced to Chile in 1982 and 1983 for pollination of red clover (Arretz & Macfarlane 1986), and by 1994 had spread to Argentina (Abrahamovich et al. 2001).

The only other group of bees to have been deliberately redistributed around the globe in substantial numbers are the Megachilidae. Perhaps because of the importance of alfalfa as a crop in the United States, a plant which is not adequately pollinated by honeybees, this country has shown particular enthusiasm for introducing exotic pollinators. The most widespread is *M. rotundata*, a native of Eurasia that appeared in North America in the 1930s, and which is now widely used commercially for pollination of alfalfa (Bohart 1972). A range of other species have been imported to pollinate various crops, including *Osmia cornuta* Latr. from Spain for pollination of almonds (Torchio 1987), *Osmia cornifrons* (Radoszkowski) from Japan for pollination of fruit trees (Batra 1979), *Osmia coerulescens* (L.) from Europe for pollination of red clover (Parker 1981), and *Megachile apicalis* Spinola from Europe for pollination of alfalfa (Cooper 1984, Stephen 1987). Furthermore, species have been moved within the United States and established in regions far from their home ranges; *Osmia ribifloris biedermannii* Michener from the west coast has been released in Maine to pollinate blueberries (Stubbs et al. 1994). At least three exotic Megachilidae are now established in California, *M. apicalis*, *M. rotundata*, and *M. concinna* (Smith) (Frankie et al. 1998), and *M. rotundata* even occurs in the Everglades National Park, Florida (Pascarella et al. 1999). New introductions continue to occur; for example *M. sculpturalis* Smith, a native of China and Japan was recently recorded in North Carolina (Mangum & Brooks 1997).

The fate of some deliberate introductions is not known. For example *Chalicodoma nigripes* from Egypt and *Pithitis smaragulda* F. from India were introduced to the United States in the 1970s for pollination of alfalfa, but to my knowledge it is not known if these species became established (Daly et al. 1971, Parker et al. 1976). One megachilid, *M. rotunda* was introduced to New Zealand in 1971 for pollination of alfalfa and flourished (Donavan 1975). Recently this species also became established in southern Australia (Woodward 1996).

One final bee that has expanded its range with the deliberate help of man is the alkali bee, *Nomia melanderi* (Cockerell) (Halictidae). This native of North America was introduced to New Zealand in 1971 for pollination of alfalfa and has become established at restricted sites (Donovan 1975, 1979). A summary of the distribution of exotic bee species is given in Table 1.

Bees are a large group (about 20,000 species are known), but little is known about basic aspects of the ecology of most species. For the majority we have only a rudimentary knowledge of their natural distribution. It is almost certain that other species have been transported by man to new locations, but that these events have gone unrecorded.

Both *B. terrestris* and *A. mellifera* are social species, with colonies attaining sizes of up to 500 and 50,000 individuals, respectively. In their natural range, nest density estimates for *A. mellifera* vary from 0.5 to >70 nests/km^2 in Europe (Visscher & Seeley 1982, Oldroyd et al. 1995) and 4.2 nests/km^2 in Botswana (McNally & Schneider 1996). Where honeybees have been introduced, estimates include 50–150 nests/km^2 in southern Australia (Oldroyd et al. 1997) and 6–100 nests/km^2 for Africanized bees in the neotropics (Roubik 1983, 1988; Otis 1991). Densities are no doubt greatly influenced by variation in habitat quality and availability of nest sites. Given the large numbers of workers per nest, even the lowest estimates indicate substantial densities of foragers. No information is available on densities of nests of *B. terrestris*, either within their natural range or where they are introduced, because they are notoriously hard to locate.

In general both honeybees and *B. terrestris* appear to maintain higher population densities than semisocial and solitary species across a broad range of habitats and geographic regions (South Australia, Pyke & Balzer 1985; California, Dobson 1993; Brazil, Wilms et al. 1997; New Zealand, Donovan 1980; Israel, Dafni 1998). It is often impossible to determine how large the equilibrium feral population of honeybees would be because wild populations are supplemented by swarms from commercial hives, and foragers observed in the field are likely to originate from both managed and wild colonies. Little information is available on populations of the introduced Megachilidae, but one study suggests that these solitary species do not attain high densities in Australia (Woodward 1996).

Because introduced bees are widespread, any deleterious effects of their presence are now occurring on a large scale. The abundance of honeybees and bumblebees makes such effects more probable. Some researchers have concluded that competition with native organisms is inevitable (Roubik 1978, Roubik & Buchmann 1984, Sugden et al. 1996).

TABLE 1 The distribution and origins of known exotic bee species

Species	Family	Introduced range	Origin	References
Apis mellifera	Apidae	North and South America, Eastern Asia, Australia, New Zealand	Eastern Europe, Western Asia, Africa	Hopkins 1911, Doull 1973, Buchmann & Nabhan 1996
Bombus terrestris	Apidae	Israel, Japan, New Zealand, Tasmania	Europe	Hopkins 1914, Dafni & Shmida 1996, Buttermore 1997, Dafni 1998, Stout & Goulson 2000
Bombus ruderatus	Apidae	New Zealand, Chile, Argentina	Europe	Hopkins 1914, Arretz & Macfarlane 1986
Bombus hortorum	Apidae	New Zealand, Iceland	Europe	Hopkins 1914, Prys-Jones et al. 1981
Bombus lucorum	Apidae	Iceland	Europe	Prys-Jones et al. 1981
Bombus subterraneus	Apidae	New Zealand	Europe	Hopkins 1914
Megachile rotundata	Megachilidae	North America, Australia, New Zealand	Eurasia	Bohart 1972, Donovan 1975, Woodward 1996, Frankie et al. 1998, Pascarella et al. 1999
Megachile apicalis	Megachilidae	United States	Europe	Cooper 1984; Stephen 1987
Megachile concinna	Megachilidae	California	Europe	Frankie et al. 1998
Megachile sculpturalis	Megachilidae	North Carolina	China, Japan	Mangum & Brooks 1997
Osmia coerulescens	Megachilidae	United States	Europe	Parker 1981
Osmia cornifrons	Megachilidae	United States	Japan	Batra 1979
Osmia cornuta	Megachilidae	United States	Europe	Torchio 1987
Osmia ribifloris biedermannii	Megachilidae	Maine	Southwestern United States	Stubbs et al. 1994
Pithitis smaragulda	Megachilidae	United States	India	Daly et al. 1971
Chalicodoma nigripes	Megachilidae	United States (establishment unknown)	Egypt	Parker et al. 1976
Nomia melanderi	Halictidae	New Zealand	North America	Donovan 1975, 1979

DIET BREADTH OF INTRODUCED BEES AND NICHE OVERLAP WITH NATIVE POLLINATORS

The diet of all bee species consists more or less exclusively of pollen and nectar collected from flowers (occasionally supplemented by honeydew, plant sap, waxes and resins, and water) (Michener 1974). The two bee species that have proved to be most adaptable in colonizing new habitats, *A. mellifera* and *B. terrestris*, have done so because they are generalists. The colonies of both species are relatively long lived and so must be able to adapt to a succession of different flower sources as they become available. *A. mellifera* usually visits a hundred or more different species of plant within any one geographic region (Pellet 1976, O'Neal & Waller 1984, Wills et al. 1990, Roubik 1991, Butz Huryn 1997, Coffey & Breen 1997), and in total has been recorded visiting nearly 40,000 different species (Crane 1990b). *B. terrestris* is similarly polylectic. It has been recorded visiting 66 native plants of 21 families in Tasmania (Hingston & McQuillan 1998) and 419 introduced and native plants in New Zealand (Macfarlane 1976). It has been argued that such statistics are misleading, because of the many flower species visited, most visits are targeted at a few favored species (Butz Huryn 1997). For example, Menezes Pedro & Camargo (1991) found that of 47 species of flower visited by honeybees in Brazil, 65% of visits were to only 9 plant species. However, even minor sources of forage for honeybees can receive substantial numbers of visits, simply because honeybees are often very abundant.

Rather less is known of the diet breadth of introduced Megachilidae. Thorp (1996) suggests that the exotic species found in California each show strong preferences for one plant family; *M. rotundata* and *M. concinna* primarily visit members of the Fabaceae, while *M. apicalis* visit Asteraceae. However, Donovan (1980) described *M. rotundata* as being polylectic in New Zealand, visiting a broad range of Fabaceae and Asteraceae.

A diverse range of different organisms collect pollen and/or nectar from flowers, including birds, bats, mammals, and insects. Of the insects, the main groups are the bees and wasps (Hymenoptera), butterflies and moths (Lepidoptera), beetles (Coleoptera), and flies (Diptera). The wide distribution and polylectic diet of most introduced bees means that potentially they might compete with many thousands of different native species. Even introduced Megachilidae no doubt overlap with many native species, because their preferred plant families are large and favored by many other flower visitors. It seems reasonable to predict that introduced bees are most likely to compete with native bee species, because these are likely to be most similar in terms of their ecological niche. Studies of niche overlap in terms of flowers visited have all concluded that both honeybees and bumblebees overlap substantially with native bees and with other flower visitors such as nectivorous birds (Donovan 1980, Roubik 1982a, Roubik et al. 1986, Menezes Pedro & Camargo 1991, Thorp et al. 1994, Wilms & Wiechers 1997, Hingston & McQuillan 1998).

Honeybees and bumblebees differ from many other flower visitors in having a prolonged flight season; honeybees remain active for all of the year in warmer climates, while bumblebees commonly forage throughout the spring and summer in the temperate climates where they naturally occur. Thus, in terms of the time of year at which they are active, they overlap with almost all other flower visitors with which they co-occur.

COMPETITION WITH NATIVE ORGANISMS FOR FLORAL RESOURCES

Demonstration of niche overlap does not prove that competition is occurring. In fact it is notoriously difficult to provide unambiguous evidence of competition, particularly in mobile organisms. Because of this there is no clear agreement as to whether non-native bees have had a significant negative impact upon native pollinator populations (compare Robertson et al. 1989, Buchmann & Nabhan 1996, Sugden et al. 1996 with Butz Huryn 1997).

The majority of studies to date have been carried out in the neotropics, stimulated by the arrival of Africanized honeybees, and in Australia, where awareness of the possible impacts of introduced species is unusually high. Australia also has a large native bee fauna of over 1500 species (Cardale 1993) that is arguably the most distinctive in the world (Michener 1965). Most work has focused on the effects of honeybees.

Effects on Foraging Behavior

Each honeybee nest harvests 10–60 kg/yr of pollen and also requires 20–150 kg/yr of honey (Stanley & Liskens 1974, Roubik et al. 1984, Buchmann 1996). Crude extrapolation from the range of nest densities that have been recorded suggests that honeybees may gather 5–9000 kg pollen and 10–22,500 kg honey km^2/yr. In New Zealand, 8000 tons of honey is harvested from about 227,000 commercial hives every year; (this does not take into account honey used by the bees themselves, or that gathered by feral colonies) (Donovan 1980). I am unaware of any estimates of the total amounts of pollen or nectar available in natural habitats over a year, and it no doubt varies enormously, but common sense suggests that honeybees must use a substantial proportion of the available floral resources.

Honeybees commonly deter other bee species from foraging on the richest sources of forage (Wratt 1968; Eickwort & Ginsberg 1980; Roubik 1978, 1980, 1996a; Wilms & Wiechers 1997; Gross 2001) (although in one instance the converse had been reported, Menke 1954). Native organisms are often displaced to less profitable forage (Holmes 1964; Schaffer et al. 1979, 1983; Ginsberg 1983). In Panama, the presence of Africanized honeybees effectively eliminated foraging peaks of Meliponine bees because these native species were prevented from visiting their preferred sources of forage; as a result, the rate at which pollen was accrued in the nest was lower (Roubik et al. 1986). Displacement of native organisms has been attributed to the larger size of honeybee when compared to the majority of bee species (Roubik 1980), but is not necessarily size related. For example, the presence of honeybees has been found to deter foraging by hummingbirds

(Schaffer et al. 1983). Similarly, in a year when honeybees were naturally scarce, native bumblebees in Colorado were found to expand their diet breadth to include flowers usually visited mainly by honeybees (Pleasants 1981).

Hingston & McQuillan (1999) examined interactions between bumblebees and native bees in Tasmania and concluded that native bees were deterred from foraging by the presence of bumblebees, perhaps because bumblebees depressed availability of floral resources. Honeybees have been shown to depress availability of nectar and pollen (Paton 1990, 1996; Wills et al. 1990; Horskins & Turner 1999), which may explain why other flower visitors then choose to forage elsewhere.

Most authors concur that honeybees are not particularly aggressive to other insects while foraging, so that impacts on other species occur primarily through exploitative competition (Schaffer et al. 1979, 1983; Thorp 1987; Roubik 1991). However, honeybees have been found to displace smaller species from flowers by physical disturbance (Gross & Mackay 1998). Honeybees do attack nests of other honey-storing species to steal the honey, a behavior that may have contributed to the decline of *Apis cerana* in Japan (Sakagami 1959).

Both honeybees and bumblebees begin foraging earlier in the morning than many native bee species (Corbet et al. 1993, Dafni & Shmida 1996, Horskins & Turner 1999). Honeybees are able to achieve this owing to their large size (compared to most bees) and also owing to heat retention within their large nests (Roubik 1989). Bumblebees are able to begin foraging earlier still because of their great size and densely hairy body. It has been argued that depletion of nectar before native bees begin to forage may result in a significant asymmetry in competition in favor of these introduced species (Matthews 1984, Hopper 1987, Anderson 1989, Dafni & Shmida 1996, Schwarz & Hurst 1997).

Asymmetries in competition may also occur because of the ability of honeybees and bumblebees to communicate the availability and/or location of valuable food sources with nest mates, so improving foraging efficiency (von Frisch 1967, Dornhaus & Chittka 1999) (the majority of bee species are solitary, and each individual must discover the best places to forage by trial and error). Thus social species are collectively able to locate new resources more quickly, which again may enable them to gather the bulk of the resources before solitary species arrive (Roubik 1980, 1981; Schwarz & Hurst 1997).

Honeybees and bumblebees appear to be unusual in the distances over which they are capable of foraging. Honeybees are known to forage over 10 km from their nest, on occasion up to 20 km (Seeley 1985, Schwarz & Hurst 1997), and *B. terrestris* up to at least 4 km (Goulson & Stout 2001). Little is known of the foraging range of most other bee species, but those estimates that are available suggest that they are generally lower. For example *Melipona fasciata* travels up to 2.4 km (Roubik & Aluja 1983) and Trigonini over 1 km (Roubik et al. 1986). Solitary bee species are generally thought to travel only a few hundred meters at most (Schwarz & Hurst 1997).

Managed honeybee hives have further advantages over wild bee species; they are often given supplementary feeds when floral resources are scarce, and they are moved to track changing patterns of floral abundance. In this way populations of honeybees may be elevated far above those that could naturally persist in particular habitats.

Asymmetries in competition may not be stable, because the relative competitive abilities of bee species are likely to vary during the day according to temperature and resource availability, and are likely to vary spatially according to the types of flowers available (Corbet et al. 1995). The main exotic bees are large compared to most of the native species with which they might compete; *B. terrestris* weighs 109–315 mg (Prys-Jones 1982), and *A. mellifera* workers 98 ± 2.8 mg (Corbet et al. 1995). They also have longer tongues than many native species, particularly in Australia where most native species are short tongued (Armstrong 1979). Large bees are at a competitive advantage in cool conditions because of their ability to maintain a body temperature considerably higher than the ambient air temperature. They can thus forage earlier and later in the day than most smaller bees, and during cooler weather. Bees with longer tongues can also extract nectar from deeper flowers. However, large bees are not always at an advantage. The energetic cost of foraging is approximately proportional to weight (Heinrich 1979). Thus large bees burn energy faster. As nectar resources decline, the marginal rate of return will be reached more quickly by large bees. Also, long tongues are inefficient at handling shallow flowers. Thus large bees are likely to be at a competitive advantage early in the day and during cool weather, and they will be favored by the presence of deep flowers that provide them with a resource that other bees cannot access. But small bees with short tongues can forage profitably on shallow flowers even when rewards per flower are below the minimum threshold for large bees.

Although in general honeybees and bumblebees are able to forage at cooler temperatures than native bees, there may be exceptions. The Australian native *Exoneura xanthoclypeata* is adapted for foraging in cool conditions (Tierney 1994). It has been argued that this species is specialized for foraging on (naturally) uncontested resources early in the day, and that this species may be particularly susceptible to competition with exotic bees that forage at the same time (Schwarz & Hurst 1997).

The outcome of interactions between exotic and native flower visitors depends upon whether floral resources are limiting. Resource availability is likely to vary greatly during the year as different plant species come into flower (Carpenter 1978). When an abundant or large plant flowers, it may provide a nectar flush. Competition is unlikely to occur during such periods (Tepedino & Stanton 1981).

Overall, it seems probable that depression of resources by introduced bees is likely to have negative effects on native bee species, at least at some times of the year. To determine whether these effects are largely trivial (such as forcing native bees to modify their foraging preferences) or profound (resulting in competitive exclusion), population-level studies are necessary.

Evidence for Population-Level Changes

The only way to test unequivocally whether floral resources are limiting is to conduct experiments in which the abundance of the introduced bee species is artificially manipulated, and the population size of native species is then monitored. If populations are significantly higher in the absence of the introduced bee, then competition is occurring. Such experiments have proved to be exceedingly hard to accomplish. Excluding bees from an area is difficult. Within- and between-season variation is likely to be large, so such experiments need to be well replicated, with replicates situated many kilometers apart, and conducted over several years. No such study has been carried out.

An alternative approach, which is far easier but provides more equivocal data, is to correlate patterns of diversity of native bees with abundance of exotic bees, without manipulating their distribution. Aizen & Feinsinger (1994) found that fragmentation of forests in Argentina resulted in a decline in native flower visitors and an increase in honeybee populations. Similarly, Kato et al. (1999) studied oceanic islands in the northwest Pacific, and found that indigenous bees were rare or absent on islands where honeybees were numerous. On Mt Carmel in Israel, Dafni & Shmida (1996) reported declines in abundance of medium- and large-sized native bees (and also of honeybees) following arrival of *B. terrestris* in 1978. Conversely, Goulson et al. (2002) found no evidence for reduced abundance or diversity of native Tasmanian bees in areas colonized by *B. terrestris*, but did find that native bee abundance was considerably higher in the few sites where honeybees were absent. However, such studies can be criticized on the grounds that the relationship between exotic bee abundance and declining native bee populations (if found) need not be causative (Butz Huryn 1997). Increasing honeybee populations are often associated with increased environmental disturbance by man, which may explain declines in native bees.

Some researchers have attempted to manipulate numbers of introduced bees, either enhancing populations in experimental plots by placing hives within them, or conversely by remove hives from experimental plots in areas where hives have traditionally been placed. Areas without hives usually still have some honeybees, since there are likely to be some feral nests, and also because honeybees can forage over great distances. Replicates of the treatment without hives need to be sited many kilometers from replicates with hives to ensure that bees do not travel between the two, so many studies have been carried out without replication (e.g., Sugden & Pyke 1991). Despite these limitations, some interesting results have been obtained. Wenner & Thorp (1994) found that removal of feral nests and hives from part of Santa Cruz Island in California resulted in marked increases in numbers of native bees and other flower-visiting insects. Addition of honeybee hives caused the Australian nectivorous bird *Phylidonyris novaehollandiae* to expand its home foraging range and to avoid parts of inflorescences favored by honeybees (Paton 1993), but a comparison of areas with and without hives found no difference in the density of this bird species (Paton 1995). Roubik (1978) found a decrease in abundance of native insects when he placed hives of the Africanized honeybee in forests in French Guiana. However, Roubik (1982a, 1983) found no consistent detrimental effects on brood size, honey, and pollen stores in nests of two Meliponine bee species in Panama when Africanized honeybee hives were placed nearby for 30 days.

Monitoring of numbers of native bee species using light traps over many years since the arrival of Africanized bee has not revealed any clear declines in abundance (Wolda & Roubik 1986, Roubik 1991, Roubik & Wolda 2001). Roubik (1996a) describes the introduction of Africanized honeybees to the neotropics as a vast experiment, but it is an experiment without replicates or controls, so interpreting the results is difficult. Sugden & Pyke (1991) and Schwarz et al. (1991, 1992a,b) failed to find clear evidence for a link between abundance of honeybees and reproductive success of anthophorid bees belonging to the genus *Exoneura* in Australia in experiments in which they greatly enhanced honeybee numbers at experimental sites. However, the native species that they studied are themselves polylectic (Schwarz & Hurst 1997). As such they are the species least likely to be affected by competition. The majority of bee species are more specialized; in a review of data for 960 solitary bee species, Schemske (1983) found that 64% gathered pollen from only one plant family, often only one genus. For example, some Australian halictine bees have only been recorded on flowers of *Wahlenbergia* sp. (Michener 1965). Very little is known about such species, and no studies have been carried out to determine whether they are adversely affected by exotic bees (Schwarz & Hurst 1997). Also, the Australian studies of Sugden & Pyke (1991) and Schwarz et al. (1991, 1992a,b) were carried out in flower-rich heathlands; floral resources are more likely to be limiting in arid regions of Australia (Schwarz & Hurst 1997), and these areas often contain the highest native bee diversity (Michener 1979, O'Toole & Raw 1991). The *Exoneura* species studied in Australia had coexisted with honeybees for 180 years, so it is not surprising that they are not greatly affected by competition with this species. If there are species that are excluded by competition with exotic bees, honeybees in particular, there is no point looking for them in places where these bees are abundant. Unfortunately this leaves rather few places where they might occur.

Overall, there is no indisputable evidence that introduced bees have had a substantial impact via competition with native species. Given the difficulties involved in carrying out rigorous manipulative experiments, this should not be interpreted as the absence of competition. The abundance of exotic bees, the high levels of niche overlap, and evidence of resource depression and displacement of native pollinators, all point to the likelihood that competition is occurring. But we do not know whether such competition results (or resulted) in competitive exclusion. The best way to test for such competition is to carry out replicated experiments in which exotic bee numbers are manipulated and native pollinator numbers and reproductive success monitored over long periods. Ideally, such studies should target native species that are not generalists, and areas where floral resources are not abundant.

COMPETITION FOR NEST SITES

Honeybees nest in cavities, usually in old trees, and there is clear potential for competition. Many other organisms, including bees, mammals, and birds use such cavities for shelter or for nesting. In managed woodland, old trees with cavities are often in short supply. Hence it seems likely that honeybees may compete with native organisms for these sites, but rigorous studies are scarce. Both Oldroyd et al. (1994) and Moller & Tilley (1989) found that nesting holes were not in limiting supply in particular forests in Victoria and New Zealand, respectively. However, both studies were confined to small geographic areas, and it is hard to draw any general conclusions without further work.

B. terrestris generally nests in existing cavities below ground, often using abandoned rodent holes (Donovan & Weir 1978), and spaces beneath man-made structures such as garden sheds (personal observation). To my knowledge there have been no studies to determine whether such sites are used by native organisms in any of the countries to which this species has been introduced, although Donovan (1980) considered it unlikely that bumblebees compete with native bee species for nest sites in New Zealand.

Megachilidae nest in small cavities in wood. Donovan (1980) reported that nests sites used by *M. rotundata* overlap with those used by native bees belonging to the Hylaeinae, and also with mason wasps and spiders in New Zealand. However, it is not known whether availability of sites is limiting. Barthell & Thorp (1995) found that introduced *M. apicalis* in California aggressively usurp native species from nests sites, and concluded that competition was likely. However, subsequent work suggested that differences in habitat preferences between native and introduced species, and an abundance of nest sites may mean that competition is weak or absent (Barthell et al. 1998). Nothing is known of niche overlap in nesting requirements between introduced Megachilidae and native species elsewhere in North America or in Australia.

TRANSMISSION OF PARASITES OR PATHOGENS TO NATIVE ORGANISMS

A great deal is known about the pathogens and parasites of honeybees, and to a lesser extent bumblebees and leafcutter bees, since these species are of economic importance. Bees and their nests support a diverse microflora including pathogenic, commensal and mutualistic organisms (Gilliam & Taber 1991, Goerzen 1991, Gilliam 1997). Many pathogens are likely to have been transported to new regions with their hosts, particularly where introductions were made many years ago when awareness of bee natural enemies was low. Thus for example the honeybee diseases chalkbrood, caused by the fungus *Ascosphaera apis*, foulbrood, caused by the bacteria *Paenibacillus larvae*, the microsporidian *Nosema apis*, and the mite *Varroa destructor* now occur throughout much of the world. Hive beetles, *Aethina tumida*, were recently transported from Africa to North America, where they are proving to be serious pests of commercial honeybee colonies (Evans et al. 2000). Similarly, bumblebees in New Zealand are host to a parasitic nematode and three mite species, all of which are thought to have come from the U.K. with the original introduction of bees (Donovan 1980). During more recent deliberate introductions of exotic bees, such as that of *N. melanderi* to New Zealand, care has been taken to eliminate pathogens or parasites before bees were released (Donovan 1979). However, parasites are easily overlooked. Queens of *Bombus ignitus* are currently sent from their native Japan to the Netherlands, where they are induced to found colonies. The colonies are then returned to Japan for commercial purposes. Goka et al. (2001) recently discovered that the returned colonies are infested with a European race of the tracheal mite *Locustacarus buchneri*.

It is hard to exaggerate our ignorance of the natural enemies of most bee species, particularly their pathogens. We do not know what species infect them, or what the host ranges of these pathogens are. Very little is known of the susceptibility of native organisms to the parasites and pathogens that have been introduced with exotic bees. In a survey of natural enemies of native and introduced bees in New Zealand, Donovan (1980) concluded that no enemies of introduced bees were attacking native bees, but that the converse was true. A chalcidoid parasite of native bees was found to attack *M. rotundata* and, rarely, *B. terrestris*. One fungus, *Bettsia alvei*, which is a pathogen of honeybee hives elsewhere in the world was recorded infecting a native bee in New Zealand, but it is not known whether the fungus is also native to New Zealand. Indeed the natural geographic range of bee pathogens is almost wholly unknown. Some bee pathogens have a broad host range; for example, chalkbrood (*A. apis*), is also known to infect *A. cerana* (Gilliam et al. 1993) and the distantly related *Xylocopa californica* (Gilliam et al. 1994). The related chalkbrood fungus *Ascosphaera aggregata* is commonly found infecting *M. rotundata*; in Canada, where *M. rotundata* is an exotic species, this fungus infects the native bees *Megachile pugnata* Say (Goerzen et al. 1992) and *M. relativa* Cresson (Goerzen et al. 1990).

It seems likely that these few recorded instances of exotic bee pathogens infecting native species are just the tip of the iceberg, since so few studies have been carried out. As to whether these pathogens have had, or are having, a significant impact on native species, we do not know; if the introduction of a new pathogen were to lead to an epizootic in native insects, it would almost certainly go unnoticed. In other better known organisms, exotic pathogens have had disastrous impacts; for example the introduction of several crayfish species from North America has led to elimination of the native species *Astacus astacus* and *Austropotamobius pallipes* from large portions of Europe. The native species have little resistance to the exotic fungal pathogen *Aphanomyces astaci* that is carried by the introduced crayfish (Butler & Stein 1985). Studies of the incidence and identity of pathogen and parasite infestations of wild populations of native bees are urgently needed.

EFFECTS ON POLLINATION OF NATIVE FLORA

Recently, concerns have been expressed that exotic bees may reduce pollination of native plants, or alter the population structure of these plants by mediating different patterns of pollen transfer to native pollinators (Butz Huryn 1997, Gross & Mackay 1998). Efficient pollination requires a match between the morphology of the flower and that of the pollinator (reviews in Ramsey 1988, Burd 1994). If there is a mismatch, then floral rewards may be gathered without efficient transfer of pollen, a process known as floral parasitism (McDade & Kinsman 1980). Specialized obligate relationship between plants and pollinators do exist (reviewed in Goulson 1999) but are the exception (Waser et al. 1996). Most flowers are visited by a range of pollinator species, each of which will provide a different quality of pollinator service.

The efficiency of honeybees as pollinators of native plants in Australia and North America was reviewed by Butz Huryn (1997). She concluded that honeybees provide an effective pollination service to the majority of the flower species that they visit, although they do act as floral parasites when visiting a small number of plant species such as *Grevillea X gaudichaudii* in Australia (Taylor & Whelan 1988) and *Impatiens capensis* and *Vaccinium ashei* in North America (Wilson & Thomson 1991, Cane & Payne 1988). Similar results have been found for honeybees visiting Jamaican flora (Percival 1974). That honeybees are effective pollinators of many plants, even ones with which they did not coevolve is not surprising. After all, they have been used for centuries to pollinate a broad range of crops. Thus pollination of the native Australian *Banksia ornata* was increased by the presence of honeybee hives (Paton 1995), and honeybees have proved to be as effective as native bees in pollinating wild cashews, *Anacardium occidentale* in South America (Freitas & Paxton 1998). However, their presence may result in reduced seed set of some native plants. Roubik (1996b) reported declining seed set in the neotropical plant *Mimosa pudica* when honeybees were the dominant visitors, compared to sites where native bees were the more abundant, while Aizen & Feinsinger (1994) found reduced pollination of a range of Argentinian plant species in areas where forests were fragmented and honeybees more abundant. Gross & Mackay (1998) demonstrated that honeybees were poor pollinators of the Australian native *Melastoma affine,* so that when honeybees were the last visitors to a flower, seed set was reduced. As Roubik (1996b) points out, if native pollinators are lost (be it through competition with exotic bees, habitat loss, or use of pesticides) then we cannot expect honeybees to provide an adequate replacement pollination service for all wild plants and crops.

No studies have yet been reported of the effects of exotic bumblebees on the seed set of native plants. *B. terrestris* has the potential to disrupt pollinator services in a different way. This bee species is known to rob flowers. When the structure of the flower renders the nectaries inaccessible, *B. terrestris* (and some other bee species) may use their powerful mandibles to bite through the base of the corolla (Inouye 1983). In this way they act as floral parasites, removing nectar without effecting pollination. In Tasmania they rob some bird-pollinated plants in this way (personal observation). The effects of this behavior are hard to predict. Robbers have been found to reduce the amount of reward available, resulting in decreased visitation rates by pollinators (McDade & Kinsman 1980) and a reduction in seed set (Roubik 1982b, Roubik et al. 1985, Irwin & Brody 1999). Robbing can damage floral tissues preventing seed production (Galen 1983). However, nectar robbing may have little influence on plant fecundity if nectar robbers also collect pollen and in doing so effect pollination, or if other pollinators are present (Newton & Hill 1983, Arizmendi et al. 1995, Morris 1996, Stout et al. 2000). Some plants may actually benefit from the activity of nectar robbers by forcing legitimate foragers to make more long-distance flights hence increasing genetic variability through outcrossing (Zimmerman & Cook 1985).

A second possible detrimental effect of exotic bees is that they may alter the population structure by effecting a different pattern of pollen transport to native pollinators. In South Australia, Paton (1990, 1993) found that honeybees extracted more nectar and pollen from a range of flower species than did birds, the primary native pollinators. However, honeybees moved between plants far less than did birds, and so were less effective in cross-pollinating, resulting in decreased seed set. Several other studies have reported that interplant movement by honeybees is lower than that of other visitors (McGregor et al. 1959, Heinrich & Raven 1972, Silander & Primack 1978). Of course other pollinators often also move small distances, and it has been argued that honeybees are not unusual in this respect (Butz Huryn 1997). However, this is not true. Workers of social bees are unusual in that they are not constrained in their foraging behavior by the need to find mates, locate oviposition sites or guard a territory. In contrast, for example, butterflies intersperse visits to flowers with long patrolling flights in which they search for mates or oviposition sites (Goulson et al. 1997). Thus honeybees, bumblebees, and other social bees do tend to engage in fewer long flights than other species (Schmitt 1980, Waser 1982). The most obvious possible effect of exotic social bees in this respect is increased self-pollination, which could result in reduced seed set if the plant is self-infertile. Reduced interpatch pollen movement could result in reproductive fragmentation of plant populations. There are at present no data available on the impact of exotic bees on the genetic structure of plant populations.

Clearly it is not possible to generalize as to the effects that exotic bees will have on seed set of native flowers. For some species they will provide effective pollination, for others they will not. Where native pollinators have declined for other reasons, for example as a result of habitat loss and fragmentation, exotic bees may provide a valuable replacement pollinator service for native flowers. Where exotic bees are floral parasites, the effect will depend on whether rates of parasitism are sufficient to deter native pollinators. Any change in seed set (including increases) of plant species within a community could lead to long-term ecological change, but such effects would be exceedingly hard to detect among the much larger environmental changes that are currently taking place.

POLLINATION OF EXOTIC WEEDS

As we have seen, both honeybees and bumblebees visit a broad range of flowers. They also appear to prefer to visit exotic flowers (Telleria 1993, Thorp et al. 1994). For example, in Ontario, 75% of pollen collected by honeybees was from introduced plants (Stimec et al. 1997). In New Zealand, *B. terrestris* has been recorded visiting 400 exotic plant species but only 19 native species (Macfarlane 1976). The three other introduced *Bombus* species also visit mainly introduced plants (Donovan 1980). In the highlands of New Zealand, honeybees rely almost exclusively on introduced plants for pollen during most of the season (Pearson & Braiden 1990). Introduced *Megachile rotunda* appear to feed exclusively on introduced plants in Australia (Woodward 1996).

Do visits by exotic bees improve seed set of weeds? In general, rather little is known of the pollination biology of non-native plants, and it is unclear whether inadequate pollination is commonly a limiting factor (Richardson et al. 2000). By virtue of their abundance and foraging preferences, exotic bees often make up a very large proportion of insect visits to weeds. For example in a site dominated by European weeds in Tasmania, honeybees and bumblebees were the major flower visitors and comprised 98% of all insect visits to creeping thistle, *Cirsium arvense* (D. Goulson, unpublished data). In North America, honeybees increase seed set of the yellow star thistle, *Centaurea solstitialis* (Barthell et al. 2001) and are the main pollinators of two important weeds, purple loosestrife, *Lythrum salicaria* (Mal et al. 1992) and *Raphanus sativus* (Stanton 1987). Donovan (1980) reports that bumblebees are major pollinators of introduced weeds in New Zealand. It thus seems obvious and inevitable that exotic bees will prove to be important pollinators of various weeds (Sugden et al. 1996).

Remarkably, this view has been challenged. It is hard to agree with the conclusions of Butz Huryn & Moller (1995) that "Although honey bees may be important pollinators of some weeds, they probably do not contribute substantially to weed problems." Butz Huryn (1997) argues that most weeds do not rely on insect pollination, either because they are anemophilous, self-pollinating, apomictic, or primarily reproduce vegetatively. This is undoubtedly true of some weed species. For example of the 33 worst environmental weeds in New Zealand (Williams & Timmins 1990), nine fall into one of these categories (Butz Huryn & Moller 1995). However, 16 require pollination and are visited by honeybees, and one is pollinated more or less exclusively by them (the barberry shrub, *Berberis darwinii*). Eight more are listed as having unknown pollination mechanisms (Butz Huryn & Moller 1995). This group includes the tree lupin, *Lupinus arboreus,* and broom, *Cytisus scoparius*, which are self-incompatible and rely on pollination by bumblebees (Stout et al. 2002, Stout 2000). It also includes gorse, *Ulex europeaus*, which is thought to depend on honeybee pollination, and in which seed set is greatly reduced by a lack of pollinators in the Chatham Islands where honeybees and bumblebees are absent (McFarlane et al. 1992). Thus at least four major weeds in New Zealand are pollinated primarily by exotic bees.

L. arboreus is currently a minor weed in Tasmania. However, seed set in areas recently colonized by *B. terrestris* has increased dramatically, and it is likely that *L. arboreus* may become as problematic in Tasmania as it is in New Zealand now that it has an effective pollinator (Stout et al. 2002). Its zygomorphic flowers have to be forced apart to expose the stamens and stigma; only a large, powerful bee is able to do this, and no such bees are native to Tasmania. *L. arboreus* is only one of many weeds in Tasmania, New Zealand, and southern Australia that originated in the temperate northern hemisphere and are coadapted for pollination by bumblebees.

Demonstrating that exotic bees increase seed set of weeds is not sufficient in itself to conclusively show that the action of the bees will increase the weed population (Butz Huryn 1997). No long-term studies of weed population dynamics in relation to the presence or absence of exotic bees have been carried out. Because most weed species are short-lived and dependent on high reproductive rates, it seems probable that seed production is a crucial factor in determining their abundance. Key factor analysis of the life history could reveal whether seed set is directly related to population size.

At present, Australia alone has 2700 exotic weed species, and the costs of control and loss of yields due to these weeds costs an estimated AU$3 billion per year (Commonwealth of Australia 1997). The environmental costs are less easy to quantify but are certainly large. Most of these weed species are at present of trivial importance. The recent arrival of the bumblebee may awake some of these “sleeper” weeds, particularly if they are adapted for bumblebee pollination. Positive feedback between abundance of weeds and abundance of bumblebees is probable, since an increase in weed populations will encourage more bumblebees, and vice versa. If even one new major weed occurs in Australia due to the presence of bumblebees, the economic and environmental costs could be substantial.

CONCLUSIONS

Both *A. mellifera* and *B. terrestris* are now abundant over large areas where they naturally did not occur. They are both polylectic, and thus use resources utilized by a broad range of native species. Various Megachilidae have been introduced to North America and one species to Australia and New Zealand, but very little is known about their impacts.

It seems almost certain that abundant and widespread exotic organisms that single-handedly utilize a large proportion of the available floral resources do impact on local flower-visiting fauna. Consider, for example, the Tasmania native bee community. One hundred and eighty years ago this presumably consisted of a large number of small, solitary and subsocial species. Over 100 species are known to be present today, and many more probably exist. Nowadays, by far the most abundant flower-visiting insects at almost every site is the honeybee, often outnumbering all other flower-visiting insects by a factor of 10 or more (D. Goulson, unpublished data). In the southeast, the second most abundant flower visitor is usually the bumblebee, *B. terrestris*. The majority of floral resources are gathered by these bees, often during the morning before native bees have become active. It is hard to conceive how the introduction of these exotic species and their associated pathogens could not have substantially altered the diversity and abundance of native bees. Unfortunately we will never know what the abundance and diversity of the Tasmanian bee fauna were like before the introduction of the honeybee. Of course the same applies to most other regions such as North America where the honeybee has now been established for nearly 400 years. It is quite possible that some, perhaps many, native bee species were driven to extinction by the introduction of this numerically dominant species or by exotic pathogens that arrived with it. Even were it practical or considered desirable to eradicate honeybees from certain areas, it would be too late for such species.

Similarly, the introduction of exotic bees must increase seed set and hence weediness of some exotic plants, particularly when, as in the case of the bumblebee in Australia, many of the weeds were introduced from the same geographic region and are co-adapted with the introduced bee.

It must be remembered that introduced bees provide substantial benefits to man in terms of pollination of crops, and in the case of the honeybee, in providing honey. These quantifiable benefits should be weighed against the likely costs. In areas where weeds pollinated by exotic bees are a serious threat, and/or where native communities of flora and fauna are particularly valued, it may be that the benefits provided by these species are outweighed by the costs. Clearly further research, particularly rigorous manipulative experiments, are needed to determine how much introduced bees contribute to weed problems and whether they do substantially impact upon native pollinator communities. The cautionary principle argues that in the meantime we should at the very least prevent further deliberate release of exotic bee species (such as of bumblebees in mainland Australia, and speculative introductions of various solitary bee species in the United States). Unlike many of the other impacts that man has on the environment, introduction of exotic species is usually irreversible. It would also seem sensible to avoid placing honeybee hives within environmentally sensitive areas where possible, particularly areas where the native flora is threatened by invasion with weed species.

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