



Do exotic bumblebees and honeybees compete with native flower-visiting insects in Tasmania?

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Abstract

Honeybees, *Apis mellifera*, have been introduced by man throughout the globe. More recently, other bee species including various bumblebees (*Bombus* spp.) have been introduced to several new regions. Here we examine the impacts of honeybees and the bumblebee, *Bombus terrestris*, on native flower-visiting insects in Tasmania. To assess whether native insects have lower abundance or are excluded in areas that have been colonised by exotic bees, we quantified the abundance, diversity and floral preferences of flower-visiting insects at sites where bumblebees and honeybees were present, and compared them to sites where they were absent. This was achieved by hand searches at 67 sites, and by deploying sticky traps at 122 sites. Honeybees were by far the most abundant bee species overall, and dominated the bee fauna at most sites. There was considerable niche overlap between honeybees, bumblebees and native bees in terms of the flowers that they visited. Sites where bumblebees were established had similar species richness, diversity and abundance of native flower-visiting insects compared to sites where bumblebees were absent. In contrast, native bees were more than three times more abundant at the few sites where honeybees were absent, compared to those where they were present. Our results are suggestive of competition between honeybees and native bees, but exclusion experiments are needed to provide a definitive test.

Introduction

Honeybees (*Apis mellifera*) (L.) (Hymenoptera; Apidae) were introduced into Australia in 1821, and are now widespread and abundant (Ziegler 1993). Honeybees have been introduced to many countries yet there is no clear agreement as to whether they have a significant negative impact upon native flower visitors (reviews in Paton (1993) and Sugden et al. (1996), Butz Huryn (1997)). There is abundant evidence that they reduce availability of nectar and pollen (Paton 1990, 1996; Wills et al. 1990; Horskins and Turner 1999) and deter other bee species from foraging on the richest nectar sources (Roubik 1978, 1980; Schaffer et al. 1979, 1983; Ginsberg 1983; Roubik et al. 1986; Wilms and Wiechers 1997).

Aizen and 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 north west Pacific, and found that indigenous bees were rare or absent on islands where honeybees were numerous, which they concluded was evidence for competitive exclusion. However, such studies can be criticised 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.

Manipulative experiments provide a more powerful means of studying competition, but are hard to

carry out with mobile organisms such as bees. Removal of honeybee hives has been shown to result in dramatic increases in abundance of native bees in California (Wenner and Thorp 1994). Roubik (1978) reported a decrease in abundance of native insects when he placed hives of the Africanized honeybee (*A. mellifera scutellata* Lepeletier) in forests in French Guiana. Later studies in Panama found that the presence of Africanized honeybees resulted in reduced foraging activity and reduced harvests of floral resources of some native social bee species, but not others (Roubik et al. 1986). However, monitoring of native bee species over many years since the arrival of Africanized bee has not revealed any clear declines in abundance (Wolda and Roubik 1986; Roubik 1991). Similarly, Sugden and Pyke (1991) and Schwarz et al. (1991, 1992) failed to find clear evidence for effects of honeybees on the reproductive success of anthophorid bees in Australia. Overall, there is no indisputable evidence that introduced bees have had a substantial impact via competition with native species, but given the difficulties involved in carrying out rigorous manipulative experiments this should not be interpreted as the absence of competition.

Honeybees are not the only exotic social bee to have been deliberately introduced to new continents by man. Bumblebees (*Bombus* spp.) are found throughout the temperate regions of the northern hemisphere, and naturally occur in the southern hemisphere only in South America (Williams 1994). Several species have recently expanded their range, either through natural dispersal (notably the invasion of Israel by *B. terrestris* (Dafni and Shmida 1996), or following introductions by man. Four species of bumblebee were deliberately introduced to New Zealand from Britain in 1885 and 1906, and became established (Hopkins 1914). Several unsuccessful attempts were made to introduce *Bombus* species into mainland Australia in the early 1900's for pollination purposes (Buttermore 1997). However, one of the species now found in New Zealand, *Bombus terrestris audax* (L.) (Hymenoptera; Apidae), recently colonised Tasmania; it was first observed in 1992 in Hobart (Semmens et al. 1993). It is assumed that the Tasmanian bumblebee population originated from the New Zealand one (Semmens et al. 1993). By January 1999 they had spread from Hobart approximately 85 km south, 55 km west, 20 km east and 65 km north (Stout and Goulson 2000).

These two exotic bee species could, either singly or in conjunction, have adverse effects on native flower-visiting insects through competition, either for floral resources (nectar and pollen) or for nest sites. This has relevance for conservationists, but is also of broader interest. The importance of interspecific competition in pollinator communities is poorly understood. Competition seems to occur between hummingbird species (Cody 1968; Feinsinger et al. 1985; Tiebout 1993) and between North American bumblebee species (Pyke 1982; Inouye 1978, 1980; Graham and Jones 1996), but studies on European bumblebees have found no such effects (Ranta et al. 1980; Ranta and Vepsäläinen 1981). To our knowledge, no studies have examined competition between bumblebees and other bee species in natural communities. Outside of their natural range, bumblebees have been found to exhibit substantial overlap in floral resource use with native bees in Tasmania (Hingston and McQuillan 1998), New Zealand (Donovan 1980) and Israel (Dafni and Shmida 1996). Hingston and McQuillan (1999) examined interactions between bumblebees and native bees in Tasmania and concluded that native bees were deterred from foraging on certain flowers by the presence of bumblebees, perhaps because bumblebees depressed availability of floral resources. It is not known if these effects lead to reductions in native bee populations.

Here we examine patterns of abundance of flower-visiting insects at a large number of sites, both within and just outside the current range of *B. terrestris*, and use these data to assess whether native bee abundance and diversity are affected by the presence of *A. mellifera* or by the addition of this new potential competitor to the community.

Methods

Distribution of Bombus terrestris and Apis mellifera

The current distribution of exotic bumblebees in Tasmania was determined by surveys carried out in January, November and December 1999. Both bumblebees and honeybees are conspicuous, and hence it is straightforward to determine whether they are present in an area by searching for them. Searches were conducted in suitable habitats, and repeated at intervals of 3–5 km along all roads leading out of the core area of the population centered on Hobart. When neither bee species was found, the search was discontinued

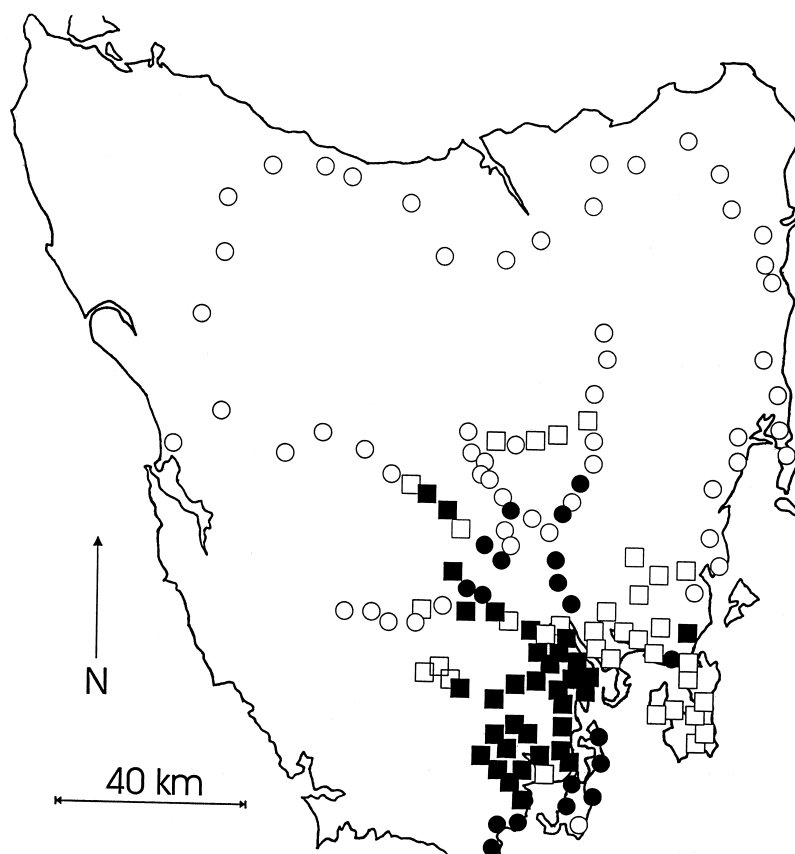


Figure 1. Sites in Tasmania where bee communities were sampled using a 30 minute search (squares), and sites which were briefly searched to detect the presence or absence of bumblebees or honeybees (circles). Filled circles/squares indicate the presence of bumblebees.

after 5 mins. The patterns obtained were consistent. Many sites were visited on several occasions, and the presence or absence of bumblebees and honeybees almost invariably remained constant. To obtain additional information on the rate of spread of bumblebees, gardeners living outside and in the periphery of the distribution were interviewed to establish whether they had seen bumblebees in their garden, and if so, in which year they first saw them.

Sampling of flower-visiting insects

Flower-visiting insects were surveyed within areas of approximately 50 m radius (the precise shape was often constrained by accessibility). All insects observed feeding on flowers, and the flower species that they were feeding upon, were recorded during a 30 min search. All searches took place between 11:00 and 15:00 h and between 15 November and 10 December 1999. Each individual insect was recorded only once as far as was possible. An attempt was made to cap-

ture all native bees for identification. Search sites were chosen to span the range of bumblebees (36 sites) and also to include areas where we were unable to find any bumblebees (31 sites) (Figure 1). All of the search sites fell in areas in which the natural vegetation type is classified as either dry sclerophyll or wet eucalypt (Jackson 1999). However, many of the sites had been heavily modified by man. Sites were classified as: gardens and parks (10 sites); pasture, weeds and waysides (32 sites); predominantly native scrub or forest (25 sites). Where flowering trees were included in the site attempts were made to sample the lower branches, but flower visitors that remained in the canopy were undoubtedly overlooked. For each plant species that was in flower, estimates were made of the number of inflorescences within each site.

To obtain additional information on the distribution and diversity of pollinating insects, yellow sticky traps (Agrisense-BCS Ltd) were deployed at 122 sites. The colour of these traps attracts flower-visiting insects, which become entangled in the glue. The 40

× 24.5 cm traps were placed at a height of approximately 1 m on the north side of tree trunks or fence posts, and were left in place for 2 weeks before collection. All sites fell within southeast Tasmania (Figure 1). The habitats where traps were placed were classified as before into gardens and parks (14 sites); pasture, weeds and waysides (70 sites); predominantly native scrub or forest (38 sites). Sixty six traps were placed within the current range of bumblebees, and 56 at sites where no bumblebees were recorded.

Bees were identified using Michener (1965) and Walker (1995), and by comparison with museum specimens held at the University of Queensland. It is probable that a number of the bees caught have yet to be described; specimens of uncertain affiliation were identified only to genus. Bees on sticky traps were identified only to genus because the glue obscured some of the distinguishing features.

Analysis

Species richness and a Shannon diversity index were calculated for all flower visitors at each of the 67 sites at which searches were conducted, and for the 122 sites at which sticky traps were deployed (exotic bees were excluded).

For the search data, three-way analysis of variance was used to test whether species richness or diversity, or the total number of native flower-visiting insects differed according to three factors: the presence or absence of bumblebees; the presence or absence of honeybees; and according to habitat type (gardens, pasture or native forest). Total numbers of insects were square root transformed before analysis. Relationships between native insect species richness, diversity and number of individuals and the number of bumblebees and honeybees present at each site were examined by Pearson product-moment correlation.

These analyses were repeated using only bee species (excluding other flower-visiting insect taxa). At one search site no bees were found, so this site was excluded from subsequent analysis. Because of the smaller number of bee species, the species richness values violated the assumptions of analysis of variance. Thus effects of the presence of bumblebees on bee species richness were examined using a Mann-Whitney U test, and differences between habitats were examined with a Kruskal-Wallis test. The relationship between species richness and bumblebee and honeybee abundance was examined using a Spearman rank correlation.

The data from sticky traps were similarly analysed. Bees made up a small proportion of the insects caught, so no separate analysis was conducted on bee species in isolation. Once again, species richness values were analysed using non-parametric tests.

Four native bee species occurred at a large number of sites: *Exoneura bicolor* (Anthophoridae), *Lasioglossum clelandi*, *Lasioglossum brunnesetum* and *Lasioglossum lanarium* (Halictidae). χ^2 tests (with Yates' correction) were used to examine whether the proportion of sites occupied by each of these species differed between areas where bumblebees occurred and where they did not. This analysis could not be carried out with respect to the presence or absence of honeybees since there were too few sites from which honeybees were absent.

One might expect rare native bee species to be more susceptible to competition with introduced bees than the abundant native species. To test whether this was so, sites at which bee species were caught that occurred at no more than two other sites were examined. A χ^2 test (with Yates' correction) was used to determine whether these tended to be sites where bumblebees did not occur. Again, this test was not performed for honeybees since they were absent from too few sites.

Niche overlap in flower usage was calculated between *B. terrestris*, *A. mellifera*, and the four most abundant native bee species, following Colwell and Futuyma (1971):

Niche overlap between bee species *i* and

$$h = 1 - 0.5\sum(P_{ik} - P_{hk})$$

Where

$$P_{ik} = \frac{\text{No. bee species } i \text{ visiting plant species } k}{\text{Total no. bee species } i}$$

Niche overlaps were calculated separately for each site.

Results

Distribution of B. terrestris and A. mellifera

Bumblebees were found to be abundant throughout a large area of southern Tasmania centered on Hobart (Figure 1). The western limits of the distribution corresponded closely with the edge of human settlement. As far as we can ascertain there were no resident

Table 1. The mean species richness, diversity (Shannon index) and number of individuals (abundance) of all flower-visiting insects according to habitat type, presence or absence of bumblebees, and presence or absence of honeybees (means \pm SE). Bumblebees and honeybees were not included in species counts or the diversity index. Reliable data were not available on the presence of honeybees at all sticky trap sites.

	Hand search data				Sticky trap data			
	Richness	Diversity index	Abundance	N	Richness	Diversity index	Abundance	N
Bumblebees absent	6.51 \pm 0.53	1.26 \pm 0.09	46.5 \pm 6.54	31	4.39 \pm 0.38	0.973 \pm 0.08	24.3 \pm 4.71	56
Bumblebees present	6.94 \pm 0.56	1.30 \pm 0.08	53.4 \pm 12.4	36	3.70 \pm 0.29	0.888 \pm 0.07	17.3 \pm 3.30	66
Honeybees absent	8.25 \pm 1.18	1.34 \pm 0.23	65.7 \pm 14.8	8	–	–	–	–
Honeybees present	6.54 \pm 0.40	1.27 \pm 0.06	48.1 \pm 8.01	59	–	–	–	–
Pasture, weeds and waysides	5.97 \pm 0.46	1.21 \pm 0.08	49.8 \pm 12.2	32	3.37 \pm 0.28	0.822 \pm 0.07	14.2 \pm 2.59	70
Gardens and parks	7.00 \pm 1.16	1.16 \pm 0.19	61.0 \pm 25.1	10	2.64 \pm 0.54	0.757 \pm 0.17	4.00 \pm 0.86	14
Native forests	7.64 \pm 0.69	1.42 \pm 0.10	46.4 \pm 6.78	25	5.71 \pm 0.39	1.18 \pm 0.08	38.3 \pm 6.81	38

bumblebee populations within the Tasmanian Wilderness World Heritage Area, although this would be exceedingly hard to prove convincingly given the inaccessible nature of this area. In the east, we were unable to locate any bumblebees on the Tasman Peninsula, an area with vegetation and rainfall that is very similar to areas south of Hobart where bumblebees are abundant (Jackson 1999). Offshore, bumblebees were abundant on Bruny Island. No changes were evident in the distribution between January and December 1999. It must be noted that we did not survey substantial areas of the island, and it is likely that some bumblebees are present outside of the range recorded in Figure 1.

In contrast to bumblebees, honeybees were present in all habitat types and all regions within the study area. They were abundant in areas of native forest and in parts of the World Heritage Area, although it was not possible to discern whether these were feral or domestic bees. The few sites where they could not be found were widely scattered.

Distribution and abundance of native flower-visiting insects

Searches

In total, 4,377 insects were recorded feeding upon flowers at the study sites, comprising 88 different species. Of these, 36 were bee species (Table 1), with the remainder consisting of Diptera (9 species), Lepidoptera (10 species), Coleoptera (18 species), Hemiptera (3 species) and Hymenoptera (other than Apoidea) (12 species). Some Thysanoptera were observed but not recorded. Of the bee species, honeybees were ubiquitous and by far the most abundant overall (Table 1). They comprised 51.0% of all bees

recorded (995 out of 1948). Furthermore, honeybees were found at 59 of the 67 search sites. At 47 of the 59 sites where they occurred, honeybees were the most common bee species. The second most abundant species overall was the native bee *E. bicolor* (20.7%; 403/1948), followed by the bumblebee (12.2%; 237/1948). The only other species found in appreciable numbers were Halictine bees belonging to the species-rich genus *Lasioglossum*.

Based on data from the 67 searches, we did not find a significant difference in the species richness of flower-visiting insects according to whether bumblebees or honeybees were present in the area sampled, according to the abundance of bumblebees or honeybees, or according to habitat (Tables 1 and 2). Diversity of flower-visiting insects did not vary significantly according to the presence or absence of honeybees or bumblebees, or according to the abundance of bumblebees or honeybees, but differed between habitats, being highest in areas of native vegetation and lowest in pasture. Overall abundance of flower-visiting insects did not vary according to the presence/absence of bumblebees or according to their abundance, and was similar in all three habitat types (Tables 1 and 2). However, there was also a greater abundance of flower-visiting insects at sites where honeybees were abundant (Table 2).

When native bee species are examined in isolation (excluding other flower visitors from the analysis), different patterns emerge (Tables 3 and 4). Notably, native bees were far more abundant at the few sites where honeybees were absent (Table 4). Native bees were more abundant at sites where bumblebees were absent, but this did not reach statistical significance.

Many of the native bee species recorded were represented by just one individual (see Table A1), sug-

Table 2. Results of analysis of variance and Pearson product-moment correlations for hand search data on richness (no. species), diversity and abundance (number of individuals) of flower-visiting insects according to the presence or absence of bumblebees and honeybees, abundance of bumblebees and honeybees, and according to habitat type.

Explanatory factor	Species Richness	Diversity	Abundance
Bumblebee presence	$F_{1,57} = 0.021, p = 0.89$	$F_{1,57} = 0.783, p = 0.38$	$F_{1,57} = 0.000, p = 0.99$
Bumblebee abundance	$r = -0.145, p = 0.24$	$r = -0.169, p = 0.17$	$r = -0.114, p = 0.36$
Honeybee presence	$F_{1,57} = 0.047, p = 0.83$	$F_{1,57} = 2.22, p = 0.14$	$F_{1,65} = 0.016, p = 0.90$
Honeybee abundance	$r = -0.051, p = 0.68$	$r = 0.118, p = 0.34$	$r = 0.309, p = 0.011$
Habitat	$F_{2,57} = 2.85, p = 0.07$	$F_{2,64} = 4.44, p = 0.016$	$F_{2,64} = 0.12, p = 0.88$

Table 3. The mean species richness, diversity (Shannon index) and number of individuals (abundance) of native bees observed in searches according to habitat type and the presence or absence of bumblebees (means \pm SE). Bumblebees and honeybees were not included in species counts or the diversity index.

	Richness	Diversity index	Abundance	N
Bumblebees absent	1.97 \pm 0.28	0.381 \pm 0.07	13.2 \pm 3.21	30
Bumblebees present	2.22 \pm 0.30	0.546 \pm 0.10	8.78 \pm 1.73	36
Honeybees absent	2.86 \pm 0.63	0.415 \pm 0.15	30.4 \pm 10.8	7
Honeybees present	2.02 \pm 0.22	0.478 \pm 0.07	8.47 \pm 1.23	59
Pasture, weeds and waysides	1.65 \pm 0.26	0.391 \pm 0.08	8.13 \pm 1.82	31
Gardens and parks	3.10 \pm 0.62	0.831 \pm 0.20	13.4 \pm 3.24	10
Native forests	2.11 \pm 0.34	0.427 \pm 0.10	13.1 \pm 3.80	25

Table 4. Results of analyses of richness (no. species), diversity and abundance (number of individuals) of native bees according to the presence or absence of bumblebees and honeybees, abundance of bumblebees and honeybees, and according to habitat type.

Explanatory factor	Species Richness	Diversity	Abundance
Bumblebee presence	$U = 520, p = 0.79$	$F_{1,58} = 0.132, p = 0.72$	$F_{1,58} = 0.16, p = 0.69$
Bumblebee abundance	$Rho = -0.027, p = 0.83$	$r = -0.048, p = 0.70$	$R = -0.176, p = 0.16$
Honeybee presence	$U = 142, p = 0.17$	$F_{1,58} = 0.090, p = 0.77$	$F_{1,58} = 21.3, p < 0.001$
Honeybee abundance	$Rho = 0.054, p = 0.67$	$r = 0.092, p = 0.46$	$R = 0.135, p = 0.28$
Habitat	$\chi^2_2 = 5.27, p = 0.72$	$F_{2,58} = 0.891, p = 0.42$	$F_{2,58} = 0.099, p = 0.91$

gesting that there are probably yet more rare species that went undetected.

Sticky trap data

Eight genera of bee were captured on sticky traps, along with 25 other insect species that visit flowers (2,516 insects in total). The diversity of species caught was significantly greater in native forest than in pasture or gardens ($F_{2,116} = 5.08, p = 0.008$) (Table 1). The same pattern was found in species richness (Kruskal Wallis test, $\chi^2 = 25.1, d.f. = 2, p < 0.001$) and in abundance of individuals ($F_{2,116} = 28.3, p < 0.001$). However, the presence or absence of bumblebee populations had no discernible effect on the diversity ($F_{1,116} = 0.38, p > 0.05$) or on the species richness of flower-visiting insects caught (Mann-Whitney $U = 1593, p = 0.19$) (Table 1). The presence

of honeybees was not assessed at all of the sticky trap sites, so the effects of honeybees on catches could not be analysed.

Distributions of abundant native bees

E. bicolor, *L. brunnesetum* and *L. lanarium* were equally likely to occur in sites where bumblebees were established and in sites where bumblebees were not found ($\chi^2_1 = 0.01, 0.01$ and 2.37 , respectively). *L. clelandi* were more likely to be found in sites containing bumblebees (19/36 sites) than where bumblebees were absent (7/31 sites) ($\chi^2_1 = 5.19, p < 0.05$).

Table 5. Numbers of the six most abundant bee species recorded in searches (totals for 62 sites), according to whether they were visiting flowers of native or exotic plants. Also shown is the total number of plant species each bee species was recorded as visiting.

	Native plants	Exotic plants	totals	% native	No. native species	No. exotic species	% visits to <i>Leontodon</i>
<i>A. mellifera</i>	273	722	995	27.4	25	41	4.52
<i>B. terrestris</i>	39	198	237	16.5	9	37	2.48
<i>E. bicolor</i>	312	91	403	77.4	13	10	1.69
<i>L. clelandi</i>	8	108	116	6.90	6	22	34.5
<i>L. lanarium</i>	4	37	41	9.76	4	5	41.5
<i>L. brunnesetum</i>	8	28	36	22.2	5	7	41.7

Distributions of rare native bees

In total, 23 of the 67 sites contained bees found at no more than two other sites. These rare bees were no more likely to be found in sites where no bumblebees were recorded (13/31 sites) than within them (10/36 sites) ($\chi^2_1 = 0.92$, $p > 0.05$). Occurrence of rare bee species was too infrequent to allow analysis by habitat type, but they were found slightly more frequently in native forest (9/25 sites) and in gardens (6/10 sites) than in pasture (8/32 sites).

Flower choice and niche overlap

In total, 1,948 bees were recorded in site searches, comprising 36 different species. These bees were recorded feeding upon the flowers of 87 different plant species, of which 32 were native species and 55 were introduced. Over all sites, there were more inflorescences of native plants (63.2%) than of introduced plants (36.8%). Despite this, both of the introduced bee species exhibited a marked preference for introduced plants, with only 16.5% of bumblebees and 27.4% of honeybees recorded on native plants (Table 5). However, only one of the four abundant native bee species, *E. bicolor*, was found mostly on native flowers; the other three *Lasioglossum* sp. were also found predominantly on introduced weeds, notably *Leontodon* sp. (Table 5).

Honeybees were recorded visiting the broadest range of flowers (66 species) with bumblebees recorded visiting 46 plant species. The more abundant native species were also polylectic, visiting between 9 and 28 plant species (Table 5). These figures reflect in part the abundance of the bees; a common species such as the honeybee is likely to be observed visiting more plant species than a rarer bee.

The niches of all species do overlap, for some flower species were visited by a broad range of na-

tive and introduced bee species. For example 17 bee species were recorded feeding on the introduced *Leontodon* sp., and 13 on the native shrub *Goodenia ovata* (Goodeniaceae). However, the flower choices of all species differ, with a maximum niche overlap of 0.68 (between the native bees *L. brunnesetum* and *L. lanarium*). Niche overlaps between native and exotic species varied between 0.17 and 0.58, indicating that there is potential for competition between these species (Table 6). However, these measures of niche overlap do not take into account whether bees were collecting pollen or nectar, or possible differences in the times of day that bee species feed, and so should be regarded as upper estimates.

Overall, the majority of bee visits were to introduced plant species (64.9%). However, the data suggest that the rarer native bees are more dependent on native flowers than the more common species. Thirteen bee species were only recorded once and, of these, ten were caught on native plant species.

Discussion

There were marked differences in the distribution of bumblebees and honeybees. Honeybees were more or less ubiquitous and abundant throughout the study area, and also elsewhere in Tasmania (D.G. pers. obs.). In contrast, we were unable to locate bumblebees at the sites we visited in the north or west of the island (although substantial areas were not surveyed). This result contrasts with that of Hingston et al. (2002), who present records gathered by a large number of amateur recorders over the 10 years since the introduction of *B. terrestris*. Their data suggest that bumblebees are present in parts of the World Heritage Area in the south west of Tasmania, and that they have recently reached the north coast. The difference probably reflects recorder effort, and the greater num-

Table 6. Niche overlap between two exotic bee species and the four most abundant native bee species. Overlaps shown are means \pm SE for all sites sampled in which each pair of species were observed foraging. Sample sizes (numbers of sites) are given in parentheses. Some pairs of species were rarely found at the same site, so that sample sizes are small; these measures of niche overlap must be interpreted with caution.

	<i>B. terrestris</i>	<i>A. mellifera</i>	<i>E. bicolor</i>	<i>L. clelandi</i>	<i>L. lanarium</i>	<i>L. brunnesetum</i>
<i>B. terrestris</i>	–					
<i>A. mellifera</i>	0.377 \pm 0.062 (22)	–				
<i>E. bicolor</i>	0.271 \pm 0.092 (14)	0.367 \pm 0.080 (22)	–			
<i>L. clelandi</i>	0.259 \pm 0.067 (20)	0.262 \pm 0.054 (26)	0.154 \pm 0.057 (10)	–		
<i>L. lanarium</i>	0.584 \pm 0.417 (2)	0.476 \pm 0.116 (11)	0.256 \pm 0.193 (5)	0.400 \pm 0.194 (5)	–	
<i>L. brunnesetum</i>	0.174 \pm 0.078 (8)	0.240 \pm 0.080 (14)	0.349 \pm 0.114 (12)	0.280 \pm 0.196 (5)	0.682 \pm 0.193 (3)	–

ber of sites that they surveyed. Hingston et al. (2002) accept a single sighting of a pollen-collecting bee, or two sightings of (perhaps the same) bees as evidence of breeding populations, which leads to their conclusion that bumblebees are now established throughout most of Tasmania. With many recorders working over many years, it is perhaps not surprising that they have accumulated records of these large, mobile organisms from throughout Tasmania. It remains to be determined whether bumblebees successfully breed throughout this area. Our observations suggest that bumblebees remain far more abundant in gardens, cultivated areas, and where there are substantial numbers of introduced plants, compared to areas of native vegetation. This is presumably because they exhibit a preference for introduced flowers.

No evidence was found for a decline in species richness or diversity in areas occupied by bumblebees, whether using data from hand searches or from sticky traps. Of the four most abundant native bee species, all were no more likely to occur in sites where bumblebees were not recorded than in sites where they were present. In fact one native species, *L. clelandi*, showed a significant positive association with the presence of bumblebees, perhaps reflecting similar habitat requirements (both species preferred introduced plants). Examination of the occurrence of rare bees, defined as those occurring at 3 or fewer sites, once again revealed no evidence of bumblebees displacing native species, since rare bees were not less likely to be found in sites where bumblebees occur than elsewhere. Thus our data do not suggest that bumblebees are having a significant impact upon native bee communities.

In contrast, we found that honeybee abundance was positively correlated with the abundance of native flower-visiting insects. This is probably because

sites with many flowers attract many honeybees and also many other insects. Conversely, a decrease in availability of floral resources due to the introduction of exotic bees could conceivably make native insects spend more time foraging, resulting in greater numbers being recorded (Paton 1996). Our results also demonstrated that sites where honeybees were absent supported greater numbers of native bees than sites where they occurred. This is suggestive of competitive displacement of native bees by honeybees.

Why might honeybees but not bumblebees have an effect on native bees? Honeybees are far more abundant and widespread than bumblebees, and have been in Tasmania for about 180 years as opposed to 8 years (at the time of our study) for bumblebees. Both exotic bees are large compared to the native Tasmanian species with which they might compete; *B. terrestris* weighs 109–315 mg (Prys-Jones 1982), and *A. mellifera* workers 98 \pm 2.8 mg (Corbet et al. 1995). They also have longer tongues than most native species, the Australia bee fauna being dominated by short tongued species (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 (Heinrich 1979). 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. Thus any native bee species that was susceptible to competition from a large, longer-tongued bee would have been excluded long ago by the introduction of honeybees, before records began. The addition of small numbers of another large long-tongued bee species (bumblebees) is perhaps unlikely to have an appreciable effect on small, short-tongued native bees (but could impact on larger nectar-gathering organisms such as birds).

Table A1. List of species of bee caught, with abundance (total numbers caught at 67 sites).

Megachilidae	
Megachilinae	
<i>Megachile maculiformis</i> Cockerell	2
<i>Chalicodoma heriadiforme</i> (Smith)	3
Anthophoridae	
Xylocopinae	
<i>Exoneura bicolor</i> Smith	403
<i>Exoneura</i> sp. 2	1
Colletidae	
Hylaeinae	
<i>Hylaeus amiculiformis</i> (Cockerell)	5
<i>Hylaeus zonalis</i> Smith	2
<i>Hylaeus honestus</i> (Smith)	1
<i>Hylaeus</i> sp. 1	1
<i>Meroglossa</i> sp. 1	3
Colletinae	
<i>Callomelitta</i> sp. 1	1
<i>Leioproctus clarki</i> (Cockerell)	1
<i>Leioproctus</i> sp. 1	1
<i>Leioproctus</i> sp. 2	2
<i>Leioproctus</i> sp. 3	2
<i>Leioproctus</i> sp. 4	1
<i>Leioproctus</i> sp. 5	1
<i>Leioproctus</i> sp. 6	1
Euryglossinae	
<i>Euhesma goodeniae</i> (Cockerell)	1
Halictidae	
Halictinae	
<i>Lasioglossum mundulum</i> (Cockerell)	16
<i>Lasioglossum repraesentans</i> (Smith)	9
<i>Lasioglossum expansifrons</i> (Cockerell)	1
<i>Lasioglossum baudini</i> (Cockerell)	17
<i>Lasioglossum brunnesetum</i> Walker	36
<i>Lasioglossum clelandi</i> (Cockerell)	116
<i>Lasioglossum asperithorax</i> (Cockerell)	4
<i>Lasioglossum lanarium</i> (Smith)	41
<i>Lasioglossum instabilis</i> (Cockerell)	1
<i>Lasioglossum</i> sp. 1	1
<i>Lasioglossum</i> sp. 2	1
<i>Lasioglossum</i> sp. 3	2
<i>Lasioglossum</i> sp. 4	1
<i>Lasioglossum</i> sp. 5	18
<i>Lasioglossum</i> sp. 6	3
<i>Homalictus</i> sp. 1	10
<i>Homalictus</i> sp. 2	7
Apidae	
Bombinae	
<i>Bombus terrestris</i> (L.)	237
Apinae	
<i>Apis mellifera</i> L.	995

Asymmetries in competition between bee species may not be stable, since the relative competitive abilities 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). 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 favoured by the presence of deep flowers that provide them with a protected 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. Thus the relative competitive abilities of different bee species are not consistent, and the strength of competition is likely to vary with time.

It is possible that bumblebees are restricted in distribution because they are inferior competitors to native bees and/or honeybees when foraging in natural vegetation. The high metabolic costs of bumblebees means that they need to obtain a large reward per flower to forage profitably. They may be restricted to areas where introduced weeds are common since many weed species have deep corollas (e.g. *Cirsium* and *Echium* spp.), providing them with a protected resource.

Of course our findings are not conclusive evidence for competition between honeybees and native bees (or for a lack of competition between bumblebees and native bees), since we have not demonstrated a causative link between honeybee presence and native bee abundance. Artificial manipulation of the distribution of these exotic bees would have provided a more powerful experimental approach, but is very difficult to achieve, and even then the results obtained are often equivocal (reviewed in Paton (1996) and Schwarz and Hurst (1997), Roubik and Wolda (2001)).

This study should not be taken as evidence that bumblebees are having no ecological impact. Other possible impacts include competition with vertebrate flower visitors (of which Australia has an unusually rich fauna), and effects on seed set of native and introduced weeds (many of which are adapted to bumblebee pollination). Recently, Stout et al. (in press) demonstrated that the introduced tree lupin *Lupinus*

arboreus, a serious environmental weed in New Zealand where it is pollinated by bumblebees, is now setting more seed in Tasmania in areas where bumblebees are present. Bumblebee populations may continue to increase and spread as they adapt to local conditions, and continued monitoring of their status would be valuable. Until more is known of the ecological effects of exotic bumblebees it seems prudent to attempt to prevent further colonisation events.

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References

- Aizen M.A. and Feinsinger P. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75: 330–351.
- Armstrong J.A. 1979. Biotic pollination mechanisms in the Australian flora – a review. *New Zealand J. Bot.* 17: 467–508.
- Buttermore R.E. 1997. Observations of successful *Bombus terrestris* (L.) (Hymenoptera: Apidae) colonies in southern Tasmania. *Aus. J. Entomol.* 36: 251–254.
- Butz Huryn V.M.B. 1997. Ecological impacts of introduced honey bees. *Quart. Rev. Biol.* 72: 275–297.
- Cody M.L. 1968. Interspecific territoriality among hummingbird species. *Condor* 70: 270–271.
- Colwell R.K. and Futuyma D.J. 1971. On the measurement of niche breadth and overlap. *Ecology* 52: 567–576.
- Corbet S.A., Saville N.M., Fussell M., Prys-Jones O.E. and Unwin D.M. 1995. The competition box: a graphical aid to forecasting pollinator performance. *J. Appl. Ecol.* 32: 707–719.
- Dafni A. and Shmida A. 1996. The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt Carmel, Israel. In: Matheson A. (ed.), *Conservation of Bees*. Academic Press, London, pp. 183–200.
- Donovan B.J. 1980. Interactions between native and introduced bees in New Zealand. *New Zealand J. Ecol.* 3: 104–116.
- Feinsinger P., Swarn L.A. and Wolfe J.A. 1985. Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecol. Monogr.* 55: 1–28.
- Ginsberg H.S. 1983. Foraging ecology of bees in an old field. *Ecology* 64: 165–175.
- Graham L. and Jones K.N. 1996. Resource partitioning and per-flower foraging efficiency in two bumble bee species. *Am. Midl. Nat.* 136: 401–406.
- Heinrich B. 1979. *Bumblebee Economics*. Harvard University Press, Harvard.
- Hingston A.B., Marsden-Smedley J., Driscoll D.A., Corbett S., Fenton J., Anderson R. et al. 2002. Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral Ecol.* 27: 162–172.
- Hingston A.B. and McQuillan P.B. 1998. Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems. *Aus. J. Ecol.* 23: 539–549.
- Hingston A.B. and McQuillan P.B. 1999. Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Aus. J. Zool.* 47: 59–65.
- Hopkins I. 1914. History of the bumblebee in New Zealand: its introduction and results. *New Zealand Department of Agriculture, Industry and Commerce* 46: 1–29.
- Horskins K. and Turner V.B. 1999. Resource use and foraging patterns of honeybees, *Apis mellifera*, and native insects on flowers of *Eucalyptus costata*. *Aus. J. Ecol.* 24: 221–227.
- Inouye D.W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology* 59: 672–678.
- Inouye D.W. 1980. The effects of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. *Oecologia* 45: 197–201.
- Jackson W.D. 1999. Vegetation types. *Vegetation of Tasmania*. In: Reid J.B., Hill R.S., Brown M.J. and Hovenden M.J. (eds), *Flora of Australia Supplementary Series No. 8*. Australian Biological Resources Study, Tasmania, Australia, pp. 1–10.
- Kato M., Shibata A., Yasui T. and Nagamasu H. 1999. Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands. *Researches on Population Ecology* 2: 217–228.
- Michener C.D. 1965. A classification of the bees of the Australian and South Pacific regions. *Bull. Am. Mus. Nat. Hist.* 130: 1–324.
- Paton D.C. 1990. Budgets for the use of floral resources in mallee heath. In: Noble J.C., Joss P.J. and Jones G.K. (eds), *The Mallee Lands: A Conservation Perspective*. CSIRO, Melbourne, pp. 189–193.
- Paton D.C. 1993. Honeybees in the Australian Environment – does *Apis mellifera* disrupt or benefit the native biota. *Bioscience* 43: 95–103.
- Paton D.C. 1996. Overview of feral and managed honeybees in Australia: distribution, abundance, extent of interactions with native biota, evidence of impacts and future research. *Australian Nature Conservation Agency*, Canberra.
- Prys-Jones O.E. 1982. *Ecological studies of foraging and life history in bumblebees*. PhD Dissertation, University of Cambridge.
- Pyke G.H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* 63: 555–573.
- Ranta E., Lundberg H. and Teräs I. 1980. Patterns of resource utilization in two Fennoscandian bumblebee communities. *Oikos* 36: 1–11.

- Ranta E. and Vepsäläinen K. 1981. Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos* 36: 28–34.
- Roubik D.W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201: 1030–1032.
- Roubik D.W. 1980. Foraging behavior of commercial Africanized honeybees and stingless bees. *Ecology* 61: 8336–8345.
- Roubik D.W. 1991. Aspects of Africanized honey bee ecology in tropical America. In: Spivak M. (ed.), *The "African" Honey Bee*. Westview Press, pp. 259–281.
- Roubik D.W., Moreno J.E., Vergara C. and Wittman D. 1986. Sporadic food competition with the African honey bee: projected impact on neotropical social species. *J. Trop. Ecol.* 2: 97–111.
- Schaffer W.M., Jensen D.B., Hobbs D.E., Gurevitch J., Todd J.R. and Valentine Schaffer M. 1979. Competition, foraging energetics, and the cost of sociality in three species of bees. *Ecology* 60: 976–987.
- Schaffer W.M., Zeh D.W., Buchmann S.L., Kleinhans S., Valentine Schaffer M. and Antrim J. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. *Ecology* 64: 564–577.
- Schwarz M.P., Gross C.L. and Kukuk P.F. 1991. Assessment of competition between honeybees and native bees. July 1991 Progress Report to the World Wildlife Fund, Australia, Project P158..
- Schwarz M.P., Gross C.L. and Kukuk P.F. 1992. Assessment of competition between honeybees and native bees. January 1992 Progress Report to the World Wildlife Fund, Australia, Project P158..
- Semmens T.D., Turner E. and Buttermore R. 1993. *Bombus terrestris* (L) (Hymenoptera, Apidae) now established in Tasmania. *J. Aus. Entomol. Soc.* 32: 346.
- Stout J.C. and Goulson D. 2000. Bumblebees in Tasmania: their distribution and potential impact on Australian flora and fauna. *Bee World* 81: 80–86.
- Stout J.C., Kells A.R. and Goulson D. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation* (in press).
- Sugden E.A. and Pyke G.H. 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Aus. J. Ecol.* 16: 171–181.
- Sugden E.A., Thorp R.W. and Buchmann S.L. 1996. Honey bee native bee competition: Focal point for environmental change and apicultural response in Australia. *Bee World* 77: 26–44.
- Tiebout H.M. 1993. Mechanisms of competition in tropical hummingbirds: metabolic costs for losers and winners. *Ecology* 74: 405–418.
- Walker K. 1995. Revision of the Australian native bee subgenus *Lasioglossum* (*Chilalictus*) (Hymenoptera: Halictidae). *Memoirs of the Museum of Victoria* 55: 1–423.
- Wenner A.M. and Thorp R.W. 1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. In: Halvorson W.L. and Maender G.J. (eds), *The Fourth Californian Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, California, USA, pp. 513–522.
- Williams P.H. 1994. Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence. *Systematic Entomology* 19: 327–344.
- Wills R.T., Lyons M.N. and Bell D.T. 1990. The European Honeybee in Western Australian kwongan: foraging preferences and some implications for management. *Proc. Ecol. Soc. Aus.* 16: 167–176.
- Wilms W. and 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.
- Wolda H. and Roubik D.W. 1986. Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology* 67: 426–433.
- Ziegler K.I. 1993. *Leatherwood Nectar Resource Management Report*. Forest and Forest Industry Council, Hobart.
- Schwarz M.P. and Hurst P.S. 1997. Effects of introduced honeybees on Australia's native bee fauna. *Victorian Naturalist* 114: 7–12.
- Roubik D.W. and Wolda H. 2001. Do competing honeybees matter? Dynamics and abundance of native bees before and after honeybee invasion. *43: 53–62.*

