COMPETITIVE INTERACTIONS BETWEEN THE INVASIVE EUROPEAN HONEY BEE AND NATIVE BUMBLE BEES

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Abstract. Biological invasions represent both an increasingly important applied problem and a tool for gaining insight into the structure of ecological communities. Although competitive interactions between invasive and native species are considered among the most important mechanisms driving invasion dynamics, such interactions are in general poorly understood. The European honey bee (*Apis mellifera*) is a widespread and economically important invader long suspected to competitively suppress many native bee species. Yet the extent to which this introduced species alters native communities remains controversial, reflecting ongoing debate over the importance of resource competition in regulating pollinator populations. I experimentally tested the effects of competition with *Apis* on colony foraging behavior and reproductive success of a native eusocial bee, *Bombus occidentalis* Greene, in coastal California. *B. occidentalis* colonies located near experimentally introduced *Apis* hives had lower mean rates of forager return and a lower ratio of foraging trips for pollen relative to nectar. Both male and female reproductive success of *B. occidentalis* were also reduced with greater proximity to introduced *Apis* hives. Reproductive success correlated significantly with measures of colony foraging behavior, most strongly with the relative allocation of foraging effort to pollen collection. This pattern suggests that *B. occidentalis* colonies exposed to competition with *Apis* experienced increased nectar scarcity and responded by reallocating foragers from pollen to nectar collection, resulting in lowered rates of larval production. These results provide evidence that *Apis* competitively suppresses a native social bee known to be an important pollinator, with the potential for cascading effects on native plant communities. This work also contributes to a greater understanding of the role competitive interactions play in pollinator communities, particularly for social bees.

Key words: Apis mellifera; *biological invasion; bumble bee; colony; competition; pollinators; reproductive success.*

INTRODUCTION

The impacts of biological invasions on native communities are an increasingly important conservation concern, with recent reviews suggesting that invasive species rank second only to habitat loss as a cause of extinctions (Ruesink et al. 1995, Wilcove et al. 1998). The study of invasions can also provide a powerful tool for elucidating community structure and species interactions (Elton 1958, Simberloff 1981, Lodge 1993). Competitive interactions between nonnative and native species are a major focus of both theoretical and applied work on invasions (Herbold and Moyle 1986, Simberloff and Stilling 1996, Parker and Reichard 1998). In spite of this interest, competitive impacts of invaders on the population dynamics or fitness of native species are often inferred but rarely measured directly (Parker and Reichard 1998). Clarifying the strength and mechanisms of competitive interactions between in-

vasive and native species can both contribute to improved management of invasions and provide insights into the role of competition in structuring communities.

The European honey bee (*Apis mellifera*, hereafter *Apis*), originally native to Eurasia, is a highly successful invader that now has a near-global distribution. An abundant, social species and generalist forager, *Apis* potentially affects a wide range of both plants and nectar or pollen feeders. Speculation that *Apis* may competitively suppress native species goes back to Darwin (1872), but few experimental studies have addressed such effects. Recent reviews vary substantially in their assessment of how existing evidence does (Sugden et al. 1996) or does not (Butz Huryn 1997) support negative impacts of *Apis*, and in Australia, the issue of whether commercial apiaries threaten native species and should be regulated is currently a focus of strong debate (Manning 1997, New 1997). Clarifying how *Apis* influences native communities is particularly of interest in light of both growing concerns over declines of many native pollinator species (Nabhan and Buchmann 1997, Allen-Wardell et al. 1998), and uncertainty about the implications of disease-driven *Apis* declines and the spread of Africanized *Apis* strains (Watanabe 1994, Nabhan and Buchmann 1997).

PLATE 1. A *Bombus* worker carrying a large pollen load, foraging on the aster *Eriophyllum stachaedifolium*, which is among the most abundant and most visited plants in coastal scrub communities. Photo credit: Rafael Arias.

In this study, I experimentally manipulated and measured the competitive impacts of this introduced social insect on the colony foraging behavior and reproductive success of a native social bee, *Bombus occidentalis* Greene, in coastal California (see Plate 1). Several previous studies suggest that *Apis* may compete with many native bee species for nectar and pollen resources. Nevertheless, the majority of this work relies on indirect evidence of competition, such as measurements of niche overlap (Donovan 1980, Wills et al. 1990, Pedro and Camargo 1991, Thorp 1996, Wilms et al. 1996) or of negative correlations between *Apis* and native bee forager abundances (Holmes 1964, Roubik 1978, Schaffer et al. 1979, 1983, Pleasants 1981, Ginsberg 1983, Corbet et al. 1995). While suggestive, such studies do not provide direct evidence that floral resources are limiting, or that *Apis* reduces the fitness or population sizes of native bees (Roubik 1986, Butz Huryn 1997). Only a handful of studies have attempted to measure the impacts of *Apis* on any aspect of reproductive success for a native bee species (Roubik 1983, Sugden and Pyke 1991, Goodell 2000), with little clear evidence of competition emerging.

In addition to constituting an important applied problem, the investigation of interactions between *Apis* and native species can provide insight into the role of competition in structuring bee communities, and more broadly, guilds of social species. Bumble bees (*Bombus* spp.), in particular, have become a classic system for the study of competition and niche partitioning (Heinrich 1976, Ranta and Lundberg 1981). However, most of this work has focused on competitive effects at the scale of individual foragers rather than that of colonies. Several studies document strong correlations between floral abundances and *Bombus* distributions (Pleasants 1981, Pyke 1982, Bowers 1985, 1986), as well as demonstrating that short-term removal of interspecific competitors can alter plant use and abundances of *Bombus* foragers (Inouye 1978). In contrast, relatively little work has directly evaluated the factors influencing colony fitness in *Bombus* under field conditions (Muller and Schmid-Hempel 1992*a*), with competitive effects often inferred from counts of foragers (Bowers 1985, 1986). Short-term experimental alterations of *Bombus* forager numbers have been used to investigate competitive interactions (Inouye 1978, Laverty and Plowright 1985), but not large-scale manipulations of colony densities. With this paucity of manipulative studies directly measuring colony fitness, the role of competition in driving population dynamics remains uncertain for this common and important guild of pollinators (Bowers 1986, Butz Huryn 1997).

Apis has been naturalized in California for ~150 years (Kraus and Page 1995). However, both feral and domesticated *Apis* populations have declined dramatically across North America over the last decade and a half due to the spread of two species of parasitic mites (Watanabe 1994, Kraus and Page 1995). This decline, although perhaps temporary, provided an opportunity to measure the strength of competitive interactions between *Apis* and *Bombus* with experimental manipulations of *Apis* density. The goal of this study was to quantify the impacts of *Apis* on colony foraging behavior, growth, and reproductive success in *Bombus*

occidentalis. In addition to assessing *Apis* impacts, I also address how well measures of colony resource intake predict colony fitness.

METHODS

Study system

Bombus is the only group of eusocial bees native to temperate and arctic North America. Colonies are annual, founded in the spring by a single queen. Following a growth phase in which the colony adds workers, brood rearing switches to production of males and daughter queens in mid-to late summer (Plowright and Laverty 1984). At peak size, *Bombus* colonies generally consist of 50–500 workers, with individual workers living two to four weeks (Heinrich 1979).

In contrast, *Apis* colonies are perennial and reproduce by fission (Seeley 1997). Colonies usually consist of 10 000–50 000 workers. Larger size and the need to store nectar and pollen for provisioning the colony through the winter make individual *Apis* colonies much more intensive resource users than *Bombus* colonies. The combination of large colonies, perennial life history, broad diet, and the ability to rapidly locate and recruit to floral resources is often cited as evidence that *Apis* is likely to competitively suppress many other bee species (Moller 1996, Schwarz and Hurst 1997).

I carried out this study in coastal scrub vegetation communities at the Landels-Hill Big Creek Reserve, located near Big Sur on the central coast of California. Although anecdotal evidence suggests that the reserve once supported large numbers of feral *Apis*, I observed none at the beginning of the study in 1998. In subsequent years feral populations appeared to partially recover. At least five species of *Bombus* occur at the study site, with *B. vosnesenskii* and *B. caliginosus* the most abundant. *B. californicus*, *B. edwardsii*, and *B. occidentalis* are also present. I chose *B. occidentalis* as a focal species because, like *Apis*, it is relatively short-tongued, and the two species are likely to overlap substantially in resource use. *B. occidentalis* is generally cited as one of the most common species in central and northern coastal California, but was not among the most abundant *Bombus* species at this site during the study. However, I observed wild populations of *B. occidentalis* in all three years.

Floral resources at Big Creek during the summer months are highly restricted to lower elevation, fog-maintained coastal scrub communities. During extensive monitoring of coastal scrub flower patches carried out concurrent with the study, >90 % of *Apis* and *Bombus* forager visits observed were to the same five plant species: *Eriophyllum stachaedifolium*, *Salvia mellifera*, *Scrophularia californica*, *Stachys bullata*, and *Phacelia malvifolia*. Overlap in plant visitation rates between *Apis* and *Bombus* averaged 51% across all three years of the study, and peaked at >80% by the end of the season in both 1999 and 2000, as increasingly dry conditions led to a lower diversity of available resources (Thomson 2001). The observed similarity in visitation patterns between *Apis* and *Bombus* suggests a high degree of overlap in their plant use at this site and a strong potential for competition.

Introduction experiment

During each of the three summers of 1998, 1999, and 2000, I introduced *Apis* colonies into three sites at Big Creek Reserve selected for proximity to coastal scrub habitats and accessibility by road. In each year, sites were located ~2 km apart. I introduced between two and three *Apis* colonies per site, each of which contained ~15,000–25,000 workers. Colonies were in place between early June and early September, which encompassed the period of greatest *Bombus* worker abundance in coastal scrub habitats at Big Creek. Due to the large scale of the study, I could not completely randomize the placement of hives, but I varied the location of *Apis* introductions between years in order to control for confounding site variability. In each year, I used one site unique to that year, and no two years shared more than one introduction site.

I placed colonies of *B. occidentalis* in artificial nest boxes along a distance gradient from each *Apis* introduction site. One *B. occidentalis* colony was located at each of three distances away from each *Apis* introduction site, for a total of nine *B. occidentalis* colonies in each year of the experiment. Due to the rugged terrain at Big Creek, the distance treatments could not be replicated exactly across sites; however, at each site I located one *Bombus* colony within 10 m of the *Apis* colonies, one ~500 m away and a third ~1000 m away. Where possible, I used the same locations for *Bombus* colonies in multiple years but altered the distance treatment. I also included *Bombus* colony location as a factor in the initial data analysis to test for any influence of underlying variability in site quality, but found no significant effects.

I used laboratory-reared colonies (Bees West, Watsonville, California) in order to minimize initial differences in colony condition. Each colony contained ~50–80 workers at the beginning of the experiment. To estimate differences in colony starting sizes, I weighed each colony prior to placement in the field (Fisher and Pomeroy 1989). I did not attempt to directly estimate worker numbers in order to minimize disturbance to the nests. I placed *B. occidentalis* colonies in the field on 23 June 1998, 3 July 1999, and 22 June 2000; these introduction dates were timed based on the appearance of *Bombus* workers in the study sites each year. It is difficult to assess how the phenology of experimental colonies compared to that of wild colonies, since the experimental colonies had already produced multiple worker broods when introduced to the field. Nevertheless, the experiment overlapped with the period of greatest observed *Bombus* worker abundances at the site, suggesting that the introduced colonies ex-

perienced reasonably realistic foraging conditions. Colonies were fed with artificial nectar for the first 48–72 h after introduction to make the transition from laboratory conditions less abrupt, as workers had no prior foraging experience. I generally left *B. occidentalis* colonies in the field until foraging activity ceased. To minimize the potential for damage to combs (see *Methods: Colony reproductive success*), I removed several late-persisting colonies when foragers were still present but no longer collecting pollen, indicating that the colony was provisioning any remaining larvae with existing stores.

Apis workers are known to forage up to 14 km away from their hive, but generally concentrate most foraging activity within a 1-km radius of the colony (Eickwort and Ginsberg 1980, Seeley 1985). Areas >1 km from the introduction sites were unlikely to be free of *Apis*, but could be expected to contain much lower densities of *Apis* foragers. Numbers of *Apis* foragers observed in monitored flower patches declined exponentially with distance in 1998, and few *Apis* were found foraging >300 m from the introduction sites (Thomson 2001). However, in 1999 and 2000 average *Apis* forager abundances did not decline strongly with distance from the introduction sites. This difference may reflect greater background densities of feral *Apis* and lower floral abundances in those years, which may have complicated the detection of introduction effects using observations of forager numbers. Characterizing the spatial distribution of *Apis* foragers is extremely difficult, even when monitoring a large number of flower patches, but the potential influence of feral colonies or longer distance foraging by introduced *Apis* is an important limitation of the experimental design. Nevertheless, such effects would bias against finding evidence of competition between *Apis* and *Bombus*, making the experiment relatively conservative.

The majority of the *B. occidentalis* colonies continued to forage and actively rear larvae for at least six to eight weeks after introduction to the field, senescing only at the end of the season in late August or early September. However, a subset of the colonies in each year experienced substantial worker mortality or ceased rearing larvae prior to the end of the season. Two colonies suffered near-complete worker mortality within a month of introduction in 1998, as did one colony in 1999 and three in 2000. I observed substantial worker mortality due to alligator lizards (*Elgaria multicarinata*) foraging at the nest entrance in three of these colonies, suggesting that predation might have been responsible for the early senescence of some colonies. I included all colonies in the analysis, regardless of whether they failed early, since the goal of the study was to assess whether competition plays an important role in driving colony reproductive success even in the presence of other potential limiting factors, such as predation. Excluding early-failing colonies in some analyses actually would have strengthened observed

treatment effects, but in no case qualitatively altered any of the results.

Colony foraging

To facilitate the monitoring of foraging activity, *B. occidentalis* workers were permitted to exit and enter the colonies only through a 15.2-cm length of clear plastic tubing, and could thus readily be observed or removed for marking (Cartar 1992). I observed foraging activity in each colony at intervals of ~10 days from the beginning of the experiment until colony senescence. For the summers of 1999 and 2000, the majority of observations were carried out using a tripod-mounted camcorder to film the colony entrance. Although a subset of workers in each colony was individually marked to measure trip times (Thomson 2001), those data are not presented here. For each bee sighted I recorded the time of entrance or exit, the marking if present, and the presence or absence of a pollen load. Workers may forage for both pollen and nectar within a single trip, although I could not visually distinguish between bees that returned with only pollen from those carrying both pollen and nectar. I therefore counted any forager returning with a pollen load (e.g., carrying more than trace amounts of pollen in the corbiculae) as a pollen forager.

Observation periods varied in length from 30–320 min, and were evenly divided between morning (0900–1300) and afternoon (1300–1800) hours. In 1998, colonies were sampled more intensively but over a shorter period of time, with observations approximately every four days for a six-week period, beginning two weeks after the colony introductions. Total observation time averaged ~25 hours per colony in 1998, 22 hours per colony in 1999, and 17 hours per colony in the drier and shorter 2000 season.

I assessed the effects of experimental treatments using two response variables. First, I calculated overall rates of forager return for each observation period as the number of bees entering the colony per minute. I also calculated a measure of relative pollen foraging effort by taking the ratio of returns with pollen to total returns. This ratio reflects the relative allocation of colony foraging effort to pollen vs. nectar collection, independent of how many workers were foraging.

Colony reproductive success

In order to estimate colony size and reproductive success, I first counted all pupal cocoons and cocoon remnants in the comb from each colony and measured their length and diameter. Although worker and male cocoons cannot be distinguished from one another, those producing new queens (gynes) are readily identifiable by their larger size (Pomeroy 1979). I classified all pupal cocoons with a diameter >11 mm as gynes, based on the observed size distribution of cocoons and published values for other *Bombus* species (Pomeroy 1979, 1981).

I tested for treatment effects on final colony size, as measured by the total number of cocoons per colony. I also used three measures of colony reproductive success based on the cocoon counts. The first, gyne number, is the total number of gyne cocoons per colony. Second, I calculated the ratio of gyne cocoons to nongyne cocoons, hereafter referred to as gyne ratio. Colony size is known to strongly influence reproductive success in *Bombus* (Owen et al. 1980, Fisher and Pomeroy 1989, Muller and Schmid-Hempel 1992*a*) and experimental colonies in this study were relatively large when introduced to the field. The fraction of the colony represented by gynes may therefore better reflect competitive effects than total gyne number. Finally, I tested for effects on the quality of gynes produced by each colony as measured by their mean pupal diameter.

Larvae of the American wax moth (*Vitula edmandsii*) damaged the combs of three colonies, destroying some pupal cocoons. *V. edmandsii* consumes wax and nest debris but not developing *Bombus* brood. It has little effect on infested colonies, but often destroys remnant combs after colony senescence (Morse 1982, Kearns and Thomson 2001). Since only part of each comb was damaged, I was still able to estimate gyne ratio as the ratio of intact gyne cocoons to total intact cocoons, but I could not directly assess gyne number or total cocoon number for these three colonies. Simply excluding damaged colonies from the analysis could bias strongly against finding an effect of *Apis* introductions, because the probability of wax-moth infestation increases with colony age (Brian 1951), and colony size and reproductive success are both positively associated with longevity (Muller and Schmid-Hempel 1992*a*). In this study, two of the three damaged combs came from the longest persisting colonies, and both were located at the distance treatment furthest from *Apis* hives. Gyne ratio was a strong predictor of total gynes for undamaged colonies ($r = 0.82$, $P < 0.0001$, $N = 23$). I therefore used gyne ratio values to estimate total gyne numbers for damaged colonies. Date of removal from the field, a measure of colony longevity, also related to gyne number, but more weakly ($r = 0.37$, $P = 0.079$, $N = 23$). I present analyses for both gyne number and gyne ratio with and without the damaged colonies. The comb of one colony was consumed by beetles and could not be included in any of the cocoon analyses.

An important limitation of both gyne number and gyne ratio as measures of reproductive success is that worker cocoons could not be distinguished from male cocoons. As a result, reductions in gyne number or ratio could reflect either lower colony reproductive success or, alternatively, a sex ratio more biased toward male production. Sex ratios in *Bombus* colonies are often strongly male-biased, and some colonies with relatively high reproductive success produce few or no gynes but many males (Owen et al. 1980, Duchateau and Velthuis 1988). To assess whether or not colony male production responded in the same way to *Apis* introductions as
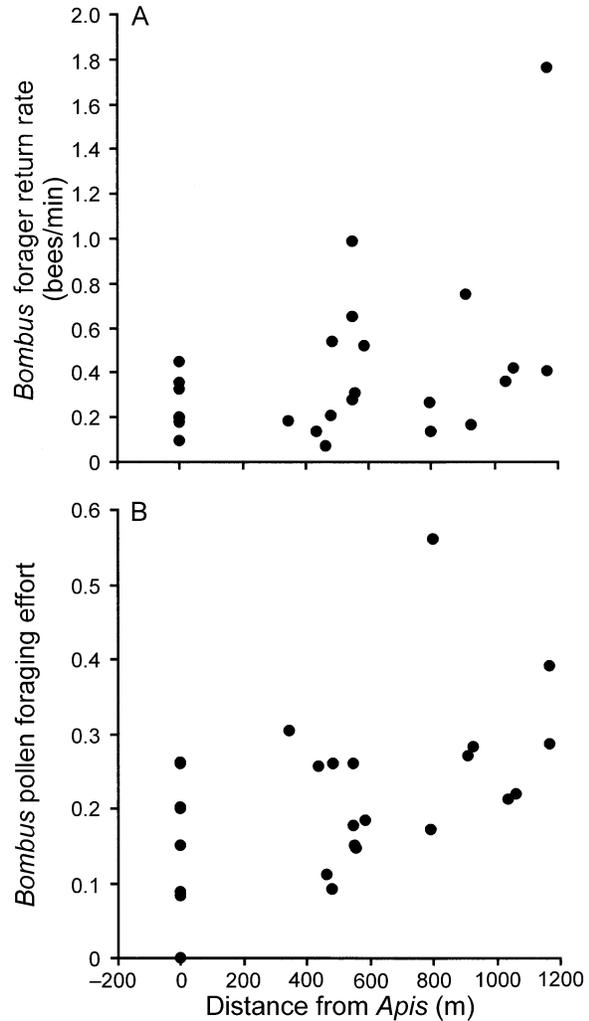

FIG. 1. Effects of distance from experimentally introduced *Apis* colonies on *B. occidentalis* colony foraging behavior, as measured by (A) mean forager return rates and (B) mean pollen foraging effort (rate of returns with pollen/total rate of returns).

gyne numbers, I used an indirect measure of relative male reproductive success based on the colony foraging observations. Males typically leave their natal colonies within a few days of emergence and do not return (Kearns and Thomson 2001), but were occasionally sighted exiting colonies during the foraging observation periods, likely in the process of dispersing. *B. occidentalis* males can be readily distinguished visually from workers based on coloration. I recorded the total number of males observed per colony for the two years in which foraging data were primarily collected by video camera, 1999 and 2000. Male numbers were corrected by the total amount of observation time per colony, to generate a rate of male sightings. I tested both for treatment effects on the rate of male sightings, and for the correlation between male sightings, gyne number, and total nongyne cocoon number to determine

TABLE 1. Effects of distance from introduced *Apis* hives on *B. occidentalis* colony foraging, tested by GLM.

Effect	SS	df	F	P
Forager return rate				
Distance from *Apis*	2.63	1	8.72	0.007**
Starting mass	0.004	1	0.013	0.91
Year	1.90	2	3.15	0.063
Error	6.64	22		
Pollen foraging effort				
Distance from *Apis*	0.078	1	10.19	0.004**
Starting mass	0.006	1	0.75	0.40
Year	0.06	2	3.94	0.035*
Error	0.17	22		

* $P < 0.05$; ** $P < 0.01$.

whether or not sex ratios appeared to vary among colonies.

Statistical analysis

Colony foraging data were not amenable to standard repeated-measures analyses because of missing observations for colonies that died earlier in the experiment and the infeasibility of sampling all colonies at the same time (von Ende 1993). I instead used mean forager return rates and pollen foraging effort for each colony across all sampling dates in a given year of the experiment. I varied the analysis slightly for the 2000 data, because four of the nine colonies, and all three of the colonies nearest to the introduced *Apis* hives, died within a month of introduction. While these colony failures may themselves have stemmed from treatment effects, they led to dramatic variability in the number and timing of forager observations for the different distance treatments. I limited the 2000 colony foraging data for this reason to the first month of the experiment, in which all nine *B. occidentalis* colonies were actively foraging for both nectar and pollen. Including all foraging observations from 2000 did not qualitatively alter any of the results presented below.

I used general linear models to test for treatment effects, with distance from *Apis* hives as a continuous independent variable, colony starting mass as a continuous covariate, and year as a categorical covariate. I log-transformed forager return rates, total cocoon number, and rate of male sightings to correct for nonnormality; all other dependent variables were analyzed untransformed, since the distributions of residuals did not differ from normal.

To explore the relationship between colony resource intake and reproductive success, I used Pearson product-moment correlations to test whether higher forager return rates and pollen foraging effort were associated with increased gyne number and gyne ratio. I excluded a single extreme outlier colony that died early in the 2000 season from this analysis.

RESULTS

Colony foraging activity

Mean forager return rates increased significantly with distance from *Apis* colonies (Fig. 1a, Table 1). Return rates were unaffected by starting size but showed some evidence of variation between years, with higher return rates in 1998 than 1999 or 2000.

Mean pollen foraging effort was also strongly reduced by proximity to *Apis* colonies (Fig. 1b, Table 1). *B. occidentalis* colonies at further distances from *Apis* hives had higher rates of forager return with pollen relative to their total return rates, suggesting that these colonies allocated a significantly higher proportion of total foraging effort to pollen collection. Like return rate, pollen foraging effort was marginally higher in 1998 than 1999 or 2000, and showed no significant relationship with starting size.

Colony reproductive success

The total number of individuals produced by *B. occidentalis* colonies, as measured by total cocoons, did not differ with distance from experimentally introduced *Apis* hives (Fig. 2, $F_{1,18} = 0.009$, $P = 0.93$). Total cocoon number was quite variable, and also showed no relationship to either starting size ($F_{1,18} = 1.55$, $P = 0.23$) or year ($F_{2,18} = 0.38$, $P = 0.09$).

In contrast, I found evidence that all four measures of colony reproductive success increased with greater distance from introduced *Apis* colonies. Gyne number of *B. occidentalis* colonies was significantly and positively related to distance when all colonies were in-
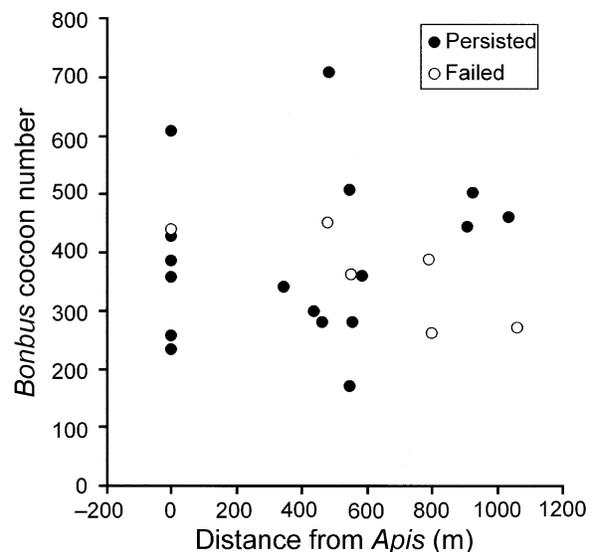

FIG. 2. Effects of distance from experimentally introduced *Apis* colonies on the total number of cocoons produced by *B. occidentalis* colonies. Open symbols represent colonies that died within 30 days of introduction, likely due to predation, and filled symbols represent colonies that persisted at least 30 days.
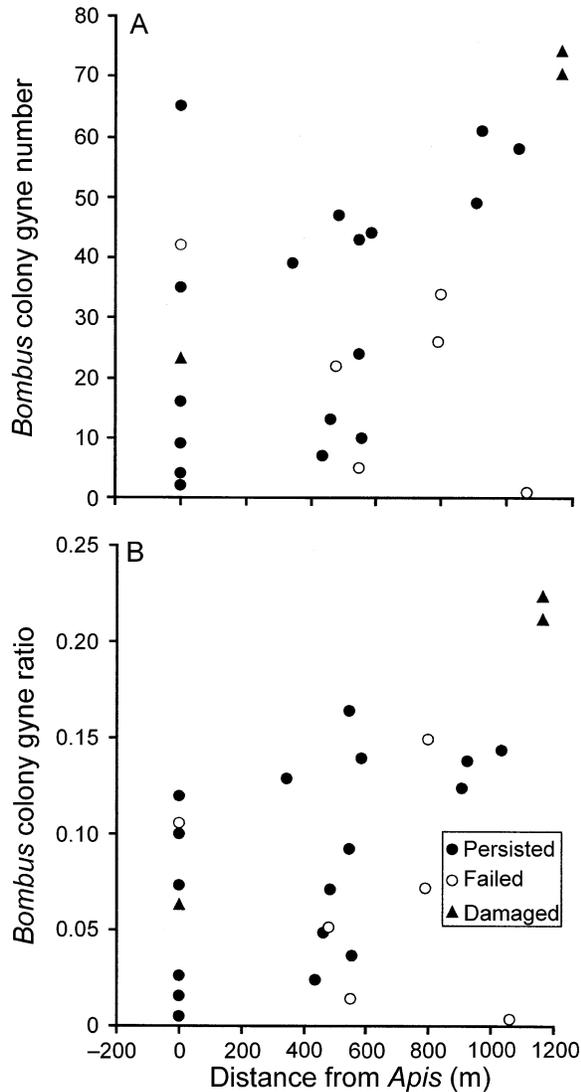
FIG. 3. Effects of distance from experimentally introduced *Apis* colonies on *B. occidentalis* colony female reproductive success, as measured by (A) colony gyne number and (B) colony gyne ratio (gyne cocoons/nongyne cocoons). Open symbols represent colonies that died within 30 days of introduction, likely due to predation, and filled symbols represent colonies that persisted at least 30 days.

cluded in the analysis, although not when estimates for damaged colonies were removed (Fig. 3*a*, Table 2). Colonies with higher starting masses reared significantly more gynes, and gyne number also varied somewhat between years, with colonies producing more gynes in 1998 than in 1999 or 2000. The effects of starting size and year were similar both with and without damaged colonies.

Gyne ratio of *B. occidentalis* colonies also increased significantly with distance from *Apis* hives (Fig. 3*b*, Table 2). As for gyne number, gyne ratio was both positively influenced by initial colony size and higher in 1998 than in 1999 or 2000. Although two of the

three damaged colonies had the highest observed values, gyne ratio showed a strong but nonsignificant trend with proximity to *Apis* hives even when these colonies were excluded from the analysis.

The mean diameter of *Bombus* gyne cocoons was significantly greater with increasing distance from *Apis* hives (Fig. 4, $F_{1,21} = 2.72$, $P = 0.012$), indicating that colonies at the further distance treatments produced gynes with greater average biomass than did those nearby *Apis* hives. Finally, the rate of male sightings per *B. occidentalis* colony increased significantly with distance from *Apis* hives (Fig. 5, $t = 2.97$, $P = 0.009$, $N = 18$). Starting size also had a positive effect on male sightings ($t = 2.41$, $P = 0.03$, $N = 18$). Overall, male sightings were rare ($N = 47$ over two years), consistent with the low probability of observing male dispersal flights even with many hours of observation.

Gyne number and the rate of male sightings per colony were positively correlated (Fig. 6, $r = 0.63$, $P = 0.007$, $N = 17$). Similarly, gyne number and the total number of nongyne cocoons (workers + males) showed a strong positive correlation ($r = 0.54$, $P = 0.008$, $N = 23$). These relationships are inconsistent with the patterns expected if colonies with higher gyne number had a lowered allocation to male production, and suggest that colonies producing greater numbers of gynes likely also had higher male reproductive success.

Colony reproductive success was positively associated with measures of colony foraging. Higher mean forager return rates correlated significantly with greater gyne number (Fig. 7*a*, $r = 0.46$, $P = 0.03$, $N = 22$). Similarly, higher gyne ratio correlated significantly with increased pollen foraging effort, (Fig. 7*b*, $r = 0.50$, $P = 0.009$, $N = 25$), a result unaltered by the exclusion of damaged colonies from the analysis.

DISCUSSION

The scarcity of demonstrated fitness or population-level effects of competition with *Apis* has been cited as evidence that many bee populations may not be limited by nectar or pollen availability (Butz Huryn 1997). In contrast, I found evidence that proximity to higher densities of *Apis* hives reduced *B. occidentalis* colony reproductive success, as measured by gyne number, gyne ratio, mean gyne size, and male sightings. Effects on gyne numbers were strongly influenced by estimates for the combs damaged by wax moths. The most conservative analysis excluding these colonies found no significant effect of proximity to *Apis* hives. However, effects of *Apis* on *B. occidentalis* gyne ratio were stronger than for gyne number and showed a nearsignificant trend even when without damaged colonies, which should represent a highly conservative test of *Apis* effects. In addition, mean gyne size and relative male reproductive success both showed clear patterns of increase with greater distance from *Apis* colonies.

There are several possible explanations for the lack of an observed treatment effect on total cocoon number,

TABLE 2. Effects of distance from introduced *Apis* hives on *B. occidentalis* gyne number and ratio, tested by GLM.

Effect	All colonies				Undamaged colonies			
	ss	df	F	P	ss	df	F	P
Gyne number								
Distance from *Apis*	2488.5	1	7.2	0.014*	603.2	1	2.14	0.16
Starting mass	2804.7	1	8.1	0.01*	3448.2	1	12.22	0.003**
Year	1970.5	2	2.8	0.081	2697.7	2	4.78	0.022*
Error	7302	21			5081.3	18		
Gyne ratio								
Distance from *Apis*	0.025	1	10.55	0.004**	0.006	1	3.59	0.074
Starting mass	0.021	1	8.86	0.007**	0.026	1	17.01	0.001**
Year	0.017	2	3.63	0.044*	0.024	2	7.74	0.004**
Error	0.05	21			0.028	18		

$* P < 0.05$; $** P < 0.01$.

in spite of the evidence for a significant relationship between distance from *Apis* and both gyne number and male sightings. First, total cocoon numbers could not be reconstructed for the damaged colonies, which necessitated the exclusion of what were likely the two biggest colonies and a large reduction in sample size at the furthest distance treatment. The exclusion of damaged colonies had a strong influence on the strength of treatment effects in the analysis of both gyne numbers and gyne ratio. Second, colonies were relatively large when placed in the field, and total cocoon number is likely to be more strongly influenced by any differences in initial worker number than gyne or male production.

Higher *B. occidentalis* gyne ratio with greater distance from *Apis* hives suggests that colonies experiencing increased competition from *Apis* generated fewer gynes per worker. Alternatively, since worker and
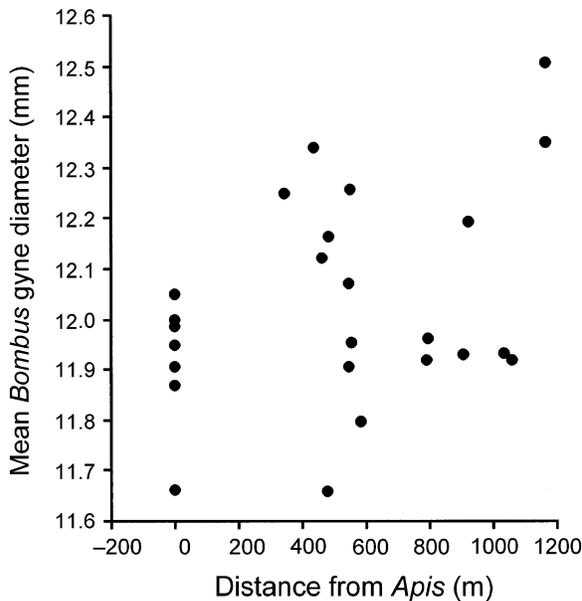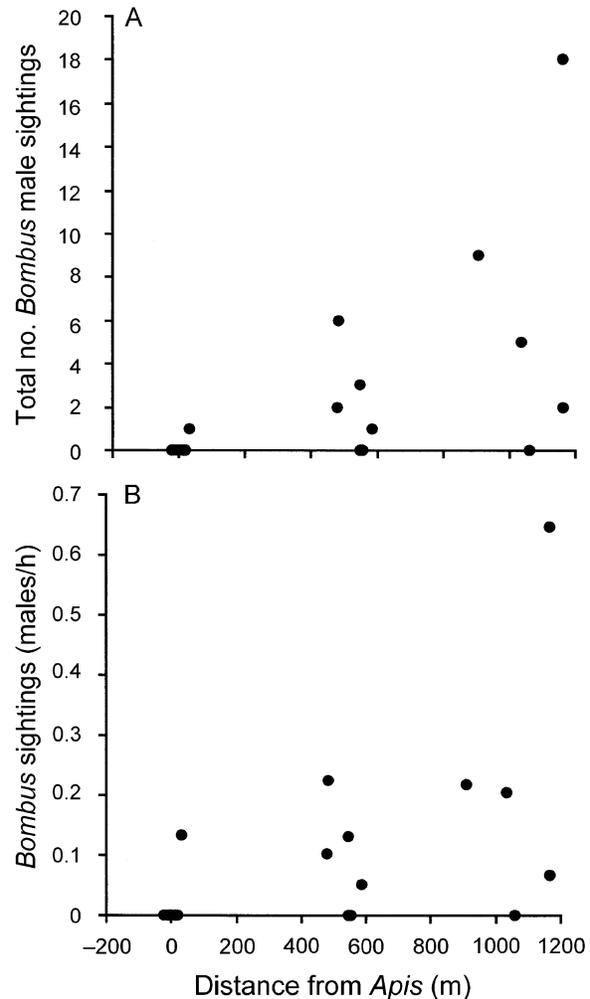

FIG. 5. Effects of distance from experimentally introduced *Apis* colonies on *B. occidentalis* colony male reproductive success, as measured by (A) the total number of male sightings and (B) rate of male sightings adjusted by total observation time. Data shown are for 1999 and 2000; video observations were not available for 1998.

FIG. 4. Relationship between mean diameter of gyne pupal cocoons and distance from introduced *Apis* colonies.
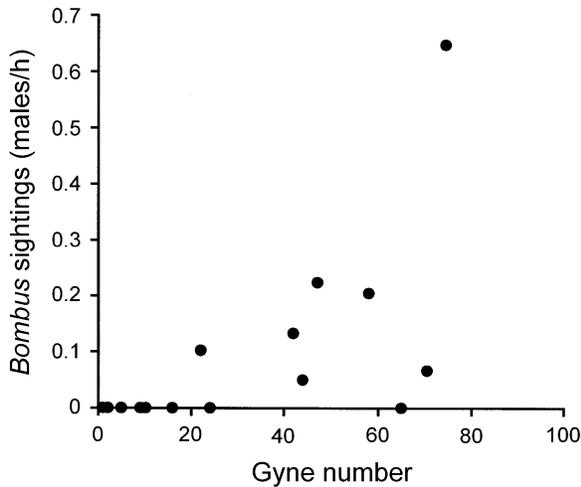
FIG. 6. Relationship between *B. occidentalis* female and
male reproductive success, as measured by gyne number and
rate of male sightings. Data shown are for 1999 and 2000;
video observations were not available for 1998.

Gynes are more costly to produce than workers and
males; for example, *B. ruderatus* queen larvae consume
twice as much pollen as do males (Pomeroy 1979). In
the absence of sex-ratio differences, a lower proportion
of gynes to workers and males implies reduced allo-
cation of resources to reproduction, relative to colony
size. Similarly, reduced gyne size in colonies nearby
Apis hives may reflect lower provisioning of larvae.
Pollen consumption is strongly correlated with pupal
diameter (Pomeroy 1979, Pomeroy and Plowright
1981), and previous work has found that food stress
generated by increased worker mortality can lead to
production of smaller gynes (Muller and Schmid-Hem-
pel 1992b). Gyne size is an important component of
reproductive success, because larger gynes are more
likely to successfully overwinter and establish colonies
(Owen 1988).

Several reasons could explain why gyne ratio showed
a stronger response to distance from *Apis* hives than
gyne number. First, gyne ratio is a less size-dependent
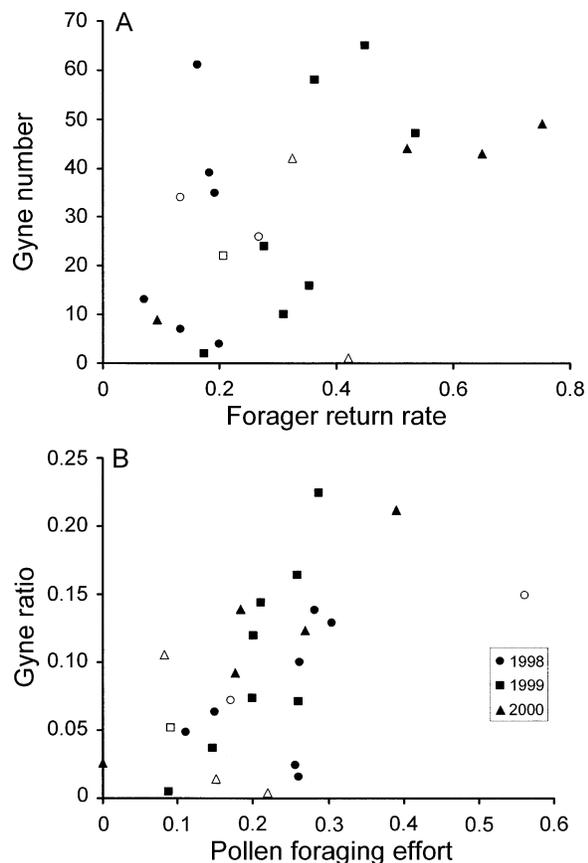measure of reproductive success than total gyne num-

male cocoons could not be distinguished, this pattern
could be attributed to a sex ratio more biased toward
males in colonies at the closer distance treatments. Sex
ratios in *Bombus* colonies are often highly male biased,
and under field conditions only a small number of the
largest colonies appear to successfully rear gynes
(Owen et al. 1980, Duchateau and Velthuis 1988, Mull-
er and Schmid-Hempel 1992a). In some cases, how-
ever, smaller, male-only colonies have been found to
produce a comparable total biomass of reproductives
as larger, gyne-producing colonies (Owen et al. 1980,
Duchateau and Velthuis 1988), while in others gyne-
rearing colonies also produce more males and have
higher total reproductive success than male-only col-
onies (Muller and Schmid-Hempel 1992a).

The strong relationship between measures of male
and female reproductive success found in this study is
consistent with the latter pattern, and makes variability
in sex ratio an unlikely explanation for the observed
differences in gyne number and ratio. Colonies that had
higher rates of male sightings also produced greater
numbers of gynes, with gyne number, gyne ratio, gyne
size, and male sightings showing similar patterns of
response across the distance treatments. Although no
males were sighted for several colonies that produced
>20 gynes, this may partly reflect the difficulty of dis-
tinguishing relatively low numbers of males from a
complete lack of male production using only direct
observations of dispersal. The factors that determine
sex ratio in *Bombus*, or cause patterns to vary across
studies, are not clearly understood, although the degree
to which colonies experience field conditions such as
food limitation may be important in driving some dif-
ferences between experiments (Muller and Schmid-
Hempel 1992a).

FIG. 7. Relationship between *B. occidentalis* colony for-
aging success and colony reproductive success, for (A) mean
forager return rate and gyne number and (B) pollen foraging
effort and gyne ratio. Open symbols represent colonies that
died within 30 days of introduction, likely due to predation,
and filled symbols represent colonies that persisted at least
30 days.

bers. Colony size is among the most important factors influencing fitness in *Bombus*, with both the probability that a colony generates reproductive castes (Muller and Schmid-Hempel 1992*a*) and the numbers of males and gynes produced (Pomeroy 1981, Fisher and Pomeroy 1989) increasing with maximum colony size. The strong effects of colony starting size on both gyne number and gyne ratio found in this study suggest that even a small amount of imprecision in accounting for differences among colonies in worker numbers at the beginning of the experiment could have partially obscured competitive effects on gyne numbers.

In addition, the relatively large size of *B. occidentalis* colonies at the beginning of the experiment likely also biased against detecting strong competitive effects on gyne number, as opposed to gyne ratio. Under field conditions, fitness in *Bombus* appears to be highly skewed, with many colonies never achieving large enough sizes to support reproduction, colonies of intermediate size producing only males, and a small number of large colonies responsible for nearly all gyne production (Muller and Schmid-Hempel 1992*a*). This suggests that factors influencing colony establishment and early-season growth are particularly important in determining ultimate reproductive success. In this study, colonies had already reached sizes of 50–80 workers by the time they were exposed to field conditions, and all colonies produced at least one queen. A limitation of the results presented here is that the large starting size of the experimental colonies may have prevented the detection of other important limiting factors affecting newly established colonies besides resource competition. At the same time, this study could also well underestimate competitive effects of *Apis* on *Bombus*, since already-established perennial *Apis* colonies may strongly suppress *Bombus* colony growth and persistence early in the season. A better understanding of colony establishment is clearly critical to a full assessment of competitive interactions. Still, with only a small fraction of the largest colonies likely to produce gynes, late-season competitive effects on the productivity of these large colonies may be particularly important to population dynamics.

Apis effects on colony foraging behavior mirror those found for reproductive success. Both return rates and pollen foraging effort were reduced by proximity to *Apis* hives. Over short time scales, colony foraging behavior can vary substantially in response to factors such as weather, forage availability, colony food stores, and larval demand (Cartar 1992, Plowright et al. 1993). Mean return rates in this study, however, encompassed a large number of observation periods from across the season. Colonies with greater return rates likely had higher average rates of resource intake (Roubik 1983), although the inability to account for differences in the size and quality of nectar and pollen loads between foraging trips is an important limitation of this measure. Higher return rates could reflect a larger worker force, shorter foraging trips, or higher larval demand due to greater rates of brood rearing. Return rates were significantly correlated with total cocoon counts and gyne number but not initial colony size, so colonies at the further distance treatments may have had higher return rates because they produced more workers or were provisioning more reproductives.

Greater pollen foraging effort with increasing distance from *Apis* hives indicates a higher investment in pollen collection over the course of the season relative to colony size. Since pollen is used primarily for provisioning larvae and nectar largely for colony maintenance and thermoregulation, lower pollen foraging effort suggests reduced allocation of colony resources to growth and reproduction. This pattern also points to nectar, rather than pollen, limitation as the most likely mechanism for the observed effects on reproductive success. Reduced pollen foraging effort suggests that *Bombus* colonies located closer to *Apis* hives experienced greater nectar scarcity, and reallocated foragers from pollen collection for larval rearing to nectar collection for meeting basic colony energy requirements. Nectar-depleted *Bombus* colonies have been shown to respond by switching foragers from pollen to nectar collection (Free 1955, Cartar 1992), and decreases in the availability of floral nectar can lead to a higher ratio of nectar to pollen foraging trips (Allen et al. 1978, Shelley et al. 1991). Colonies experiencing shortfalls in both nectar and pollen simultaneously also may enhance nectar collection at the expense of pollen, perhaps because nectar depletion potentially threatens colony persistence (Cartar and Dill 1991, Plowright and Silverman 2000). Pollen availability plays a critical role in determining larval development times (Sutcliffe and Plowright 1990) and adult size (Plowright and Jay 1977, Plowright and Pendrel 1977, Sutcliffe and Plowright 1988), in addition to the total amount of brood reared by a colony (Pomeroy and Plowright 1981). Over the long run, reductions in pollen intake due to a reallocation of foraging could be expected to impact colony reproductive success, and the strong correlation between pollen foraging effort and gyne ratio suggests that this was the case. In conjunction with fewer male sightings, lower gyne ratios in colonies with reduced pollen foraging effort may indicate that more workers were needed to provision a given number of reproductives in these colonies.

Observed patterns of floral resource availability and bee visitation are also consistent with an important role for nectar limitation in this system. Both *Apis* and *Bombus* predominately visited *Eriophyllum stachaedifolium*, an abundant perennial aster that produces relatively low-quality nectar but copious pollen. Bees are particularly dependent on *E. stachaedifolium* during drier years and at the end of the summer, when other floral resources are less abundant and competition is likely to be strongest (Thomson 2001). The amount of time individual workers spent on foraging trips for nec-

tar alone increased strongly both between morning and afternoon and from beginning to end of the season, while the lengths of foraging trips for pollen were much more constant (Thomson 2001); this suggests that workers experienced greater difficulty in acquiring nectar than pollen as forager densities increased diurnally and seasonally.

Interestingly, competitive effects may have been moderated by predation, which led to the early mortality of some colonies. I have also observed lizards consuming workers at the entrances of wild nests, although predation rates on the experimental colonies may have been elevated by placement in aboveground nest boxes. *Bombus* foragers are known to experience mortality rates ranging from 20% to 40% per week from weather and predators at flowers (Rodd et al. 1980, Muller and Schmid-Hempel 1992*b*). However, most studies of *Bombus* colony growth and fitness have focused on the role of parasites (e.g., Schmid-Hempel and Schmid-Hempel 1998) rather than nest predators. Nest predation may warrant more attention as a potential regulating factor for *Bombus*.

Overall, measures of colony resource intake were significantly correlated with colony size and reproductive success, in spite of predation effects. Colonies with greater foraging success had higher reproductive success, supporting the importance of resource limitation in determining fitness. Nevertheless, measures of colony resource intake explained a relatively low amount of the observed variance in reproductive success. This suggests reason to be cautious in utilizing monitoring of foraging behavior alone to predict the importance of competitive effects.

In spite of a long history of research on the role of competition for floral resources in driving the foraging behavior of pollinators in general and social bees in particular (e.g., Heinrich 1979, Eickwort and Ginsberg 1980), little work has explored whether or how interactions among foragers scale up to influence colony or population dynamics. Bees represent a useful system for achieving a mechanistic understanding of competitive interactions, since resource availability and forager behavior, growth, and reproductive success can all be measured (Thomson et al. 1987). Nevertheless, few studies have directly assessed the factors that influence *Bombus* colony reproductive success under field conditions, or simultaneously quantified individual or colony foraging behavior and colony growth or reproduction. The results of this work provide support for the importance of resource competition in driving colony fitness, and not just individual foraging behavior, but also suggest that factors such as predation may mediate competitive effects at the colony scale.

Studies clarifying when short-term resource depletion or competitive effects of an invader are likely to be important for native species fitness or population dynamics are particularly important in the context of monitoring invasive species impacts. In many cases,

directly demonstrating population-level competitive effects of invaders will be difficult. This creates a need for caution in inferring the presence or absence of competition, as well as clearer evaluation of when and how monitoring of parameters such as forager abundances can be used to extrapolate competitive effects at the population scale. Indeed, the evidence for effects of *Apis* on the reproductive success of native bees provided by this and other recent work (Goodell 2000) is all the more striking because such impacts have long remained uncertain in spite of substantial research attention.

This work supports the idea that *Apis* does competitively suppress some species of native bees known to be important pollinators, with the potential for cascading effects on native plant communities. To date, few studies have explored the impacts of *Apis* introduction on plants, although there is some evidence that *Apis* may both reduce seed set of certain native plants by displacing more efficient pollinators (Paton 1997, Gross and Mackay 1998) and facilitate seed production of some invasive species (Barthell et al. 2001). *Apis* potentially could also provide indirect benefits to native plants, by displacing other pollinators from more preferred resources onto less abundant or attractive species. The impacts of introduced ants are a far more recognized example of the threats posed by invasive social insects (Williams 1994) and the potential for such species to disrupt native mutualisms (Christian 2001), but the implications of pollinator introductions may also warrant greater attention.

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