

Role of Honey Bees (Hymenoptera: Apidae) in the Pollination Biology of a California Native Plant, *Triteleia laxa* (Asparagales: Themidaceae)

S. A. CHAMBERLAIN¹ AND R. A. SCHLISING

Department of Biological Sciences, California State University, Chico, CA 95929-0515

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ABSTRACT A central focus of pollination biology is to document the relative effectiveness of different flower visitors as pollinators. Ongoing research seeks to determine the role that introduced honey bees (*Apis mellifera* L.) play in the pollination of both invasive and native plants. Here we report on the importance of *A. mellifera* as pollinators of a California native plant, *Triteleia laxa* Benth. In observation plots and transect censuses, *A. mellifera* overwhelmingly dominated the *T. laxa* flower visitor assemblage. We believe the proximity to agriculture, where *A. mellifera* density is higher relative to areas far from agriculture, contributes to the discrepancy between *A. mellifera* abundance at the two sites. Although *A. mellifera* were inferior flower visitors qualitatively (visited less flowers per minute), they were the most frequent interactors with flowers. Furthermore, the proportion of visits to flowers on the same plant among flower visitor species did not differ, suggesting a general mechanism by which insects forage at *T. laxa* flowers and that *A. mellifera* do not cause more deleterious geitonogamy than do native pollinators. Flower visitation rates as a function of floral display size did not differ between *A. mellifera* and other flower visitors. The difference in the magnitude of flower visitation (largely by *A. mellifera*) between sites is consistent with a difference in seed set between sites. These results suggest that non-native *A. mellifera* bees can play an important role in the pollination of native plant species.

KEY WORDS *Apis mellifera*, honey bee, invasive species, native plant, *Triteleia laxa*

Invasive species are a major cause of species extinction and environmental degradation (Mack et al. 2000). Often invasive species are not economically beneficial, making eradication desirable. However, when invasive species form mutualisms with native and non-native species in the introduced range, the overall impact of the invader becomes complicated. *Apis mellifera* L. (the western honey bee) has been introduced around the globe to pollinate crops and provide honey and is a conspicuous visitor to many native plant species. The economic benefits in agricultural pollination by *A. mellifera* are enormous (e.g., \$14.6 billion in 2000 in the United States, Morse and Calderone 2000), whereas the negative consequences of *A. mellifera* facilitating spread of invasive plants continue to emerge. For example, widespread impacts on an entire community may occur if *A. mellifera* facilitates invasion of keystone invasive plants (e.g., yellow starthistle, *Centaurea solstitialis* in California; Barthell et al. 2001; see also Simpson et al. 2005). Although Butz Huryn (1997) posits that *A. mellifera* do not benefit invasive plants, she assumes that most invasive plants are not insect pollinated and thus do not depend on insect pollination for reproduction. Contrary to this

assumption, many invasive plants are indeed insect pollinated (Goulson 2003). The role of *A. mellifera* as pollinators of native plants is less clear.

Whether *A. mellifera* generally have negative or positive effects on native plants and pollinators is still debated (Butz Huryn 1997, Paine 2004). A recent review suggested that invasive pollinators often have negative effects on native plant-pollinator mutualisms (e.g., decrease seed set, male fitness, and population growth in native plants; Traveset and Richardson 2006; see also Gross and Mackay 1998, Kenta et al. 2007). Some studies have shown that *A. mellifera* often decrease flower visitation by native bees (Roubik 1978, Gross 2001), but no studies have documented local extinction of native bees caused by *A. mellifera* (Moritz et al. 2005). However, *A. mellifera* could facilitate spread of native plants previously limited by availability of pollinators (Gross 2001, Dick et al. 2003). For example, in an Amazonian tropical tree, *Dinizia excelsa* (Fabaceae), African honey bees (*Apis mellifera scutellata*) linked individual plants in fragments with those in continuous forest populations, thereby expanding genetic neighborhood area. Given the ongoing decline of native pollinators and the recent decline of *A. mellifera* (Buchmann and Nabhan 1995, Committee on the Status of Pollinators in North

¹ Corresponding author, e-mail: schamber@rice.edu.

America, National Research Council 2007), there is a need for more studies addressing the role of *A. mellifera* in native plant pollination.

Recently, the traditional idea that plant–pollinator interactions are typically specialized has been overturned; in fact, most plants and pollinators are relatively generalized (Waser et al. 1996). Indeed, studies of mutualistic (plant–pollinator, plant–seed disperser) communities suggest that most pairwise species interactions are relatively weak (i.e., small per capita effect of a species interaction), with a small number of strong interactions (Bascompte and Jordano 2007; but see Dicks et al. 2002). If interactions involving *A. mellifera* and native plants are weak (as a result of extreme generalist foraging of *A. mellifera*), *A. mellifera* impacts on native pollination mutualisms may be negligible (Traveset and Richardson 2006). However, even though *A. mellifera* may interact weakly averaged over the range of a plant species, weak interactions often show the greatest variation in total effect (Berlow 1999). In other words, because weak interactions averaged over a large scale can be geographically variable and locally strong (Berlow 1999), plant species may sometimes depend strongly on a generalist pollinator species such as *A. mellifera*. Geographically variable interactions between *A. mellifera* and native plants are especially likely given locally dense concentrations of managed honey bees.

Here we describe the role of the non-native *A. mellifera* in the pollination of a native California perennial, *Triteleia laxa* Benth (Themidaceae). First, we examine the composition of flower visitors to *T. laxa* within observation plots and transects. Second, there are generally two components considered when evaluating how “good” a pollinator is: quantity and quality. Quantity is the abundance of a particular flower visitor (Herrera 1989), whereas quality is, for example, the amount of pollen deposited on a stigma (Herrera 1987). We contrast the quality of flower visits (e.g., time spent in a single flower) by common flower visitors. Third, we determine how different flower visitors respond to *T. laxa* floral display. Last, we examine how flower visitation (number of visits per plot) varies in relation to mean percent seed set. Our results suggest that *A. mellifera* are important pollinators of *T. laxa*, and we discuss the circumstances under which *A. mellifera* may be important pollinators of other native plants.

Materials and Methods

Study Areas and Study Species. Two study areas were used during the months of March and April 2003 and 2005. “Park” is within Bidwell Park, on the east side of Chico, CA (39°46′42.8″ N, 121°45′10.8″ W) at ≈99-m elevation. The vegetation there is savanna, with a sparse overstory of *Quercus douglasii* Hooker and Arnot, with abundant bunchgrass *Nassella pulchra* (A. Hitchcock) Barkworth present in the herbaceous layer. “Vina” is ≈16 km north of Chico, in extreme northern Butte County (39°52′46.6″ N, 121°58′34.5″ W) at 52 m in elevation, at the Vina Plains Preserve

(owned and managed by the California Nature Conservancy). The vegetation there is rolling grassland with many forbs. The climate at both sites is typical mediterranean, with cool, wet, winter half-years alternating with hot, dry summers. An average of 555 mm of rain precipitation falls in this area, mostly between November and May (NOAA 2005). These study areas are described in detail in Schlising and Chamberlain (2006).

Triteleia laxa (Ithuriel’s spear) is a native geophyte found in the mediterranean climate region of California. *T. laxa* is widespread from sea level to 1,500-m elevation and is most common in low elevation savannas and grasslands. In our study areas, the perennating corm of *T. laxa* first produces two long, grass-like leaves during the cool and rainy mediterranean winter season and then a single flowering stem (23–32 cm high) bearing an umbel with large bluish trumpet-shaped flowers in the spring as the rainy season ends. Mean percent fruit and seed set are low (range: percent fruit set, 50–74%; percent seed set, 40–58%; Schlising and Chamberlain 2006) and vary among sites and years. Plants are largely self-incompatible. However, a previous study showed that hand self-pollination results in a mean of ≈1.4 seeds per fruit compared with hand outcross pollination, which resulted in ≈11.7 seeds per fruit (Schlising and Chamberlain 2006). After seed production, above ground activity ceases during the summer months (Schlising and Chamberlain 2006).

Insects were identified to the lowest taxonomic level possible using Hurd (1955), Hurd and Michener (1955), Thorp et al. (1983), Vockeroth and Thompson (1987), and Michener (2000). Specimens are kept at Rice University in the personal collection of the first author (S.A.C.). All plant names follow Hickman (1993).

Flowering Phenology. One 30-m transect through a population of *T. laxa* at Vina was used to record flowering phenology from flower buds to ripe fruits on 60 randomly chosen plants. The number of buds and flowers per plant and percent fruit and seed set per plant were determined. The extent of matching between flowering and flower visitation among different pollinators was visually compared.

Flower Visitor Observation Plots. We chose a single, large population of *T. laxa* at both Vina and Park sites to quantify flower visitation in 2003 and 2005. Observers sat on stools ≈1 m away from randomly placed 1-m² plots, without casting a shadow on the plot and presumably not affecting the visiting insects. In 2005, on each of 6 (Vina) and 8 (Park) d, we recorded the number and identity of flower visitors to six observation plots during each of four 2-h time periods per day (1000–1200, 1200–1400, 1400–1600, and 1600–1800 hours), for a total of 102 (Vina) and 138 (Park) plots during 2005. In addition, we recorded the number and identity of flower visitors for 18 plots at each of Vina and Park in 2003. We used analysis of variance (ANOVA) to study the effects of site, date, time of day, and floral display (number of open flowers that appeared to have available pollen and/or nectar) on

mean flower visits per plot (total visits/flowers per plot). Before analysis, data from plots within daily time periods (e.g., 1000–1200 hours) were averaged to avoid pseudoreplication. Plants per plot and flowers per plot were highly correlated (Pearson correlation coefficient, $r = 0.8$; $P < 0.00001$; $N = 240$), so only the variable with greater explanatory power (flowers per plot) was included in the final model. Temperature and humidity were measured but were not included in the final model because early exploratory analyses showed no relationship of these variables to flower visitation. Mean visits per plot was square-root transformed before analysis to meet assumptions of normality and homogeneity of variance (JMP 5.1.2; SAS Institute 2004).

Flower Visitor Transects. We surveyed *T. laxa* flower visitors along belt transects (140 m long, 3 m wide), walking at a slow, consistent pace, at both Vina and Park. On each of 6 (Vina) and 7 d (Park), transects were surveyed during each 2-h time period (1000–1200, 1200–1400, 1400–1600, and 1600–1800 hours), for a total of 20 (Vina) and 25 (Park) data points. Flower visitors were mostly easy to identify on the wing or while alighting on flowers, in which case their visits were recorded. Unknown flower visitors were captured and later identified. We used ANOVA to study the effects of the variables site, date, time of day, and visitor type on flower visitor abundance (number of individuals per transect census). Flower visitor abundance was ln-transformed before analysis to meet assumptions of normality and homogeneity of variance (JMP 5.1.2; SAS Institute 2004). No interactions were significant and thus were not included in the final model (all $P > 0.4$).

Response to Floral Display. Using the data from observation plots, we used multiple regression to evaluate the response of *A. mellifera* versus all other flower visitors to floral display, with floral display (number of flowers per plot), visitor type (*A. mellifera* versus all others), and the interaction between floral display and visitor type as explanatory variables. Number of visits per plot, floral display, visitor type, and floral display \times visitor type interaction were ln-transformed to meet assumptions of normality and homogeneity of variance (JMP 5.1.2; SAS Institute 2004).

Potential for Geitonogamy. Geitonogamy is pollination of flowers by pollen from other flowers on the same plant (de Jong et al. 1993). In *T. laxa*, we have shown, using hand-pollination experiments, that geitonogamy produces very little seeds relative to out-cross pollination (mean \pm SE seeds per fruit: geitonogamy, 1.4 ± 0.7 ; xenogamy, 11.7 ± 1.6 ; open pollination, 15.3 ± 1.4 ; Schlising and Chamberlain 2006). Using observation plot data, we studied the tendency for different flower visitors to visit flowers in a fashion that could increase geitonogamy. The percent of bouts (a sequence of flower visits among many plants by a single flower visitor) that contained visits to multiple flowers within an inflorescence was calculated separately for *Battus philenor hirsuta* (Skinner) (Papilionidae, Lepidoptera), *Autographa californica* (Speyer) (Noctuidae, Lepidoptera), *Apis*

mellifera, *Bombus vosnesenskii* Radoszowski (Apidae, Hymenoptera), and two syrphid flies (*Sphaerophoria* sp., and *Scaeva pyrastris* L.; Syrphidae, Diptera). In addition, using a χ^2 test (JMP 5.1.2; SAS Institute 2004), we compared the mean number of flowers per plant for plants that received visits to multiple flowers within an inflorescence to those plants that did not (regardless of visitor identity).

Flower Visitor Quality. We compared the quality of four species of visitors to the flowers of *T. laxa*, *A. mellifera*, *B.p. hirsuta*, *Osmia* sp. (Megachilidae, Hymenoptera), and *Papilio glaucus rutulus* Lucas (Papilionidae, Lepidoptera), at Vina (20 April 2003) and Park (11 and 18 April 2003). Two people followed each flower visitor: one person with stopwatch that also recorded times and one person observing each flower visitor. No times were recorded for visitors that merely contacted a petal without contacting anthers or the pistil. Care was taken not to follow too closely as to affect the path of the flower visitor. Only flower visitor paths with 10 or more plants visited are included in analyses. Four response variables were analyzed: visitation rate (number of flowers visited per min), handling time (time contacting a flower), flight time (time between flower contacts, whether within or between plants), and flowers visited per plant. Handling time and flight time were ln-transformed, and flowers visited per plant was square root transformed to meet assumptions of normality and homogeneity of variance (JMP 5.1.2; SAS Institute 2004). Results for *B.p. hirsuta* and *A. mellifera* timing were compared by *t*-tests.

Flower Visitation in Relation to Seed Set. In 2003 and 2005 at Vina and Park, we measured plant reproduction variables of flowers and fruits per plant, ovules per ovary, and percent seed set. We contrast percent seed set (number of seeds/number of ovules + seeds) at both sites to flower visitation in observation plots in both 2003 and 2005. Non-normal and heteroscedastic residuals required use of nonparametric Wilcoxon tests to test the hypothesis that flower visitation differed between Vina and Park; this was done separately for 2003 and 2005. We used *t*-tests to test the hypothesis that percent seed set differed between Vina and Park; this was done separately for 2003 and 2005.

Results

Flower Visitors in Relation to Site, Date, and Time. In transects, a total of 16 and 12 insect taxa were recorded visiting flowers of *T. laxa* at Park and Vina, respectively (Table 1). Additional *T. laxa* flower visitors were found during opportunistic searches at Park and Vina but were not abundant. *A. mellifera* was by far the most abundant flower visitor in both transects and observation plots. *A. mellifera* visited a wide array of forbs other than *T. laxa*, including, for example, *Convolvulus*, *Delphinium*, *Dichelostemma*, *Erodium*, *Geranium*, *Lasthenia*, *Triteleia hyacinthina* (Lindley) E. Greene, and *Vicia*. *B.p. hirsuta* was the next most common visitor to *T. laxa* flowers but was much less

Table 1. Insects recorded visiting flowers of *T. laxa* during transects, observation plots, and opportunistic collections

Flower visitor	Transects ^a			Observation plots ^b		
	Park	Vina	Total	Park	Vina	Total
Hymenoptera						
<i>Apis mellifera</i> L. (Apidae)	178	270	448	177/242	267/373	444/615
<i>Bombus edwardsii</i> Cresson (Apidae)	1		1			
<i>Bombus vosnesenskii</i> Radoszkowski (Apidae)	4	1	5	10/13		10/13
<i>Chelostoma</i> sp. (Megachilidae) ^c			—			—
<i>Eucera</i> (<i>Synhalonia</i>) sp. 1, female (Apidae)	11		11			
<i>Eucera</i> (<i>Synhalonia</i>) sp. 1, male (Apidae)	7	2	9			
<i>Eucera</i> (<i>Synhalonia</i>) sp. 2 (Apidae)	1		1			
<i>Halictus</i> sp. (Halictidae)		7	7			
<i>Lasioglossum</i> (<i>Dialictus</i>) sp. (Halictidae)	2	9	11			
<i>Lasioglossum</i> (<i>Lasioglossum</i>) sp. (Halictidae)	11	4	15			
<i>Nomada</i> sp. (Apidae)	1		1			
<i>Osmia</i> sp. (Megachilidae)	21		21	1/1		1/1
Lepidoptera						
<i>Autographa californica</i> (Speyer) (Noctuidae)	3	7	10		14/20	14/20
<i>Battus philenor hirsuta</i> (Skinner) (Papilionidae)	66	10	76	11/15	4/5	15/20
<i>Coenonympha tullia</i> (Mller) (Nymphalidae) ^c			—			—
<i>Papilio glaucus rutulus</i> Lucas (Papilionidae) ^c			—			—
<i>Scaeva pyrastris</i> (L.) (Syrphidae)	8	4	12	3/4	5/5	8/9
<i>Vanessa cardui</i> L. (Nymphalidae)	4	39	43			
Diptera						
<i>Dalmanina blaisdelli</i> Cresson (Conopidae) ^c			—			—
<i>Helophilus</i> sp. 1 (Syrphidae)	1		1			
<i>Helophilus</i> sp. 2 (Syrphidae)		1	1			
Muscidae sp.	1		1			
<i>Sphaerophoria</i> sp. (Syrphidae)		5	5	1/1	6/7	7/8
<i>Oligodranes</i> sp. (Bombyliidae) ^c			—			—

Males and females are lumped unless otherwise noted.

^a Numbers are abundance. N: belt transects of equal length and width censused 25 (Park) and 20 (Vina) times.

^b Numbers are no. of visitors/no. of total visits to flowers. N: 1,380 (Park) and 1,020 (Vina) min of observation.

^c Opportunistically collected (i.e., not found in transects or observation plots) visiting *T. laxa* flowers; all only present at Park.

abundant than *A. mellifera*. In addition to *T. laxa*, *B.p. hirsuta* often visited species of *Delphinium*, *Dichelostemma*, *Eriodictyon*, *Petrorhagia*, *Triteleia bridgesii* (S. Watson) Greene, *T. hyacinthina* (Lindley) Greene, and *T. liliacina* Greene. We observed on a few occasions large *Xylocopa tabaniformis* Smith (Apidae, Hymenoptera) nectar-robbing flowers of *T. laxa* at Park. However, *X. tabaniformis* were not abundant enough to warrant further consideration.

On two occasions in 2003 (1600–1630 hours, 18 April; 1100–1230 hours, 22 April), *B.p. hirsuta* individuals visiting *T. laxa* flowers were captured and checked for easily recognizable blue *T. laxa* pollen on various

body parts and subsequently released. Sixteen of 19 (84%) individuals carried *T. laxa* pollen, whereas 1 of the 19 carried the pollen of *Dichelostemma multiflorum* (Bentham) A.A. Heller as well. Pollen was carried on the ocular setae, frontoclypeus, labial palps, antennae, proboscis and other facial sclerites, and setae. *A. mellifera* carried pollen on various parts of the body, but the large majority of pollen was stored in corbiculae. No pollen was found on two other lepidopteran visitors (*Autographa californica* and *Vanessa cardui* L.), despite their pubescent vestiture.

Flower visitor abundance in transects varied significantly with visitor type, site, and date (Table 2; Figs.

Table 2. Multifactor ANOVAs for the influence of multiple factors on mean no. of visits per plot (all flower visitors combined; observation plots), and flower visitor abundance (transects)

Source of variation	Observation plots				Transects			
	SS	df	F	P	SS	df	F	P
Model	19.5	7	7.9	<0.0001	42.9	6	12.7	<0.0001
Site	6.3	1	17.6	<0.0001	2.8	1	5.0	0.0272
Date	0.4	1	1.1	0.3054	4.4	1	7.8	0.0062
Time of day	5.5	3	5.2	0.0029	0.7	1	1.2	0.2642
Floral display	2.1	1	6.0	0.0170	—	—	—	—
Site × date	6.9	1	19.6	<0.0001	—	—	—	—
Visitor type	—	—	—	—	38.2	3	22.5	<0.0001
<i>A. mellifera</i> versus other insects	—	—	—	—	36.1	1	63.7	<0.0001
Error	23.8	67			56.6	100		

A planned contrast was done for *A. mellifera* versus all other flower visitors for transect data. Only those interactions that were significant are shown.

Floral display, mean no. of flowers per plot; visitor type, *A. mellifera*, other bees, flies, and lepidopterans

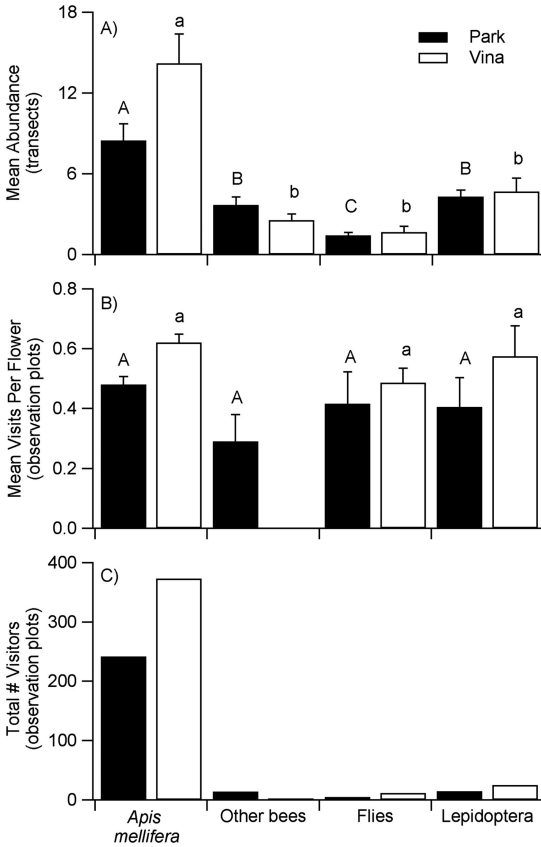


Fig. 1. *Triteleia laxa* flower visitor composition as determined by transects (A) and observation plots (B and C) at two sites: Park and Vina in 2005. (A) Mean (\pm SE) flower visitor abundance censused during transects. Bars that share uppercase (Park) or lowercase (Vina) letters are not significantly different at $P < 0.05$ (Tukey honestly significant difference test [HSD]; $N = 21, 16, 7,$ and 17 [Park] and $N = 19, 9, 6,$ and 12 [Vina] for *A. mellifera*, other bees, flies, and Lepidoptera, respectively). (B) Mean (\pm SE) number of visits per flower during observation plots. Bars that share uppercase (Park) or lowercase (Vina) letters are not significantly different at $P < 0.05$ (Tukey HSD test; $N = 52, 2, 4,$ and 8 [Park] and $N = 67, 0, 5,$ and 4 [Vina] for *A. mellifera*, other bees, flies, and Lepidoptera, respectively). (C) Total number of flower visitors to observation plots. Note that most of the bees were *A. mellifera*.

1 and 2), but did not vary with time of day (Table 2). *A. mellifera* was significantly more abundant than all other flower visitors (planned contrast, $F_{1,100} = 63.7$, $P < 0.0001$; Table 2; Fig. 1A). In observation plots, total flower visitation varied significantly with mean flowers per plot, site, and time of day (Table 2; Fig. 1). Although visitation did not vary significantly with date overall (Table 2), the difference between sites in flower visitation depended on date (Table 2; Fig. 2C).

***Apis mellifera* versus Other Flower Visitors.** *Apis mellifera* abundance was far greater relative to other flower visitors at both sites in transect censuses (Fig. 1A), and that finding is mirrored in flower visitation rates measured in observation plots (Fig. 1C). How-

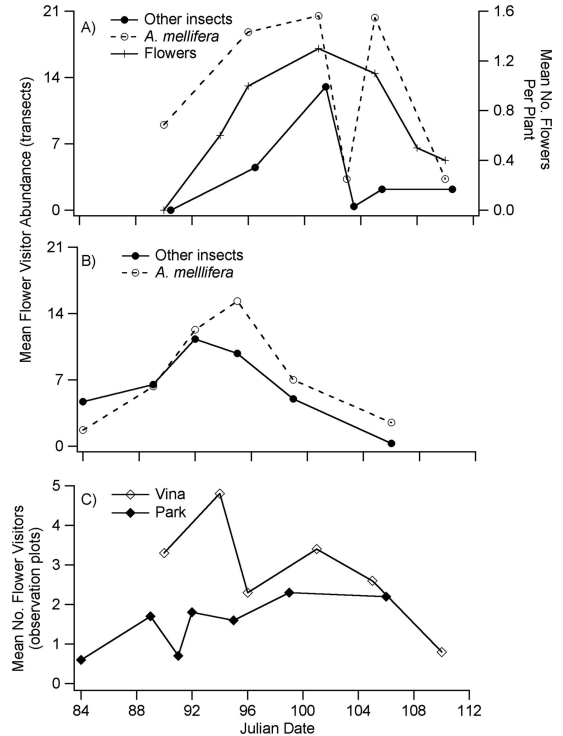


Fig. 2. Flower visitor composition of *A. mellifera* and all other insects through time. (A) Abundance of flower visitors along transects at Vina (with mean number of flowers per plant). (B) Abundance of flower visitors along transects at Park. Note that flowering phenology data are not shown for this site. (C) Mean flower visitation to observation plots at Vina and Park. Note the abscissa is Julian date (days from 1 January).

ever, these findings do not translate into greater mean visitation on a per flower basis (Fig. 1B). At Park, *A. mellifera* was significantly more abundant than other bees, whereas other bees were not more abundant than moths and butterflies, but bees, moths, and butterflies were each more abundant than flies (Fig. 1A). At Vina, *A. mellifera* was more abundant than other visitors, and abundance did not vary among other visitors (Fig. 1A).

Total visitation to observation plots was heavily dominated by *A. mellifera* (Fig. 1C), with 87 and 91% of visits to flowers by *A. mellifera* at Park and Vina, respectively. However, from an individual flower's perspective, greater *A. mellifera* abundance does not mean greater visitation (Fig. 1B). Nonetheless, *A. mellifera* is likely effecting far more pollination in *T. laxa* than other flower visitors through their high abundance.

Last, we combined all plots for both sites to analyze overall visitation response to floral display. There was a highly significant effect of floral display and visitor type on total visits per plot (overall model, $r^2 = 0.78$, $F_{3,138} = 30.0$, $P < 0.0001$; Fig. 3). As the size of floral display increased, total visits per plot increased ($F_{1,138} = 194.3$, $P < 0.0001$), and the magnitude of *A.*

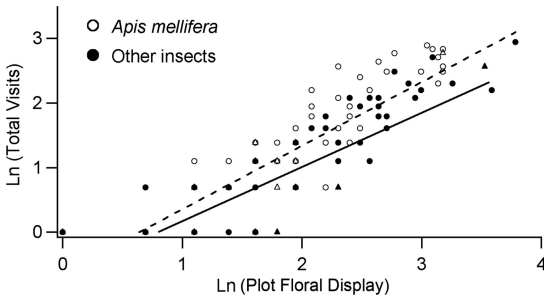


Fig. 3. Total flower visitation in observation plots (each point is an individual 1-m² plot) as a function of floral display (flowers per plot) and flower visitor type (*A. mellifera* [open circles, dashed line] versus all other insects [solid circles, solid line]). Lines are best fit linear regression. Slopes of the two lines are not statistically different.

mellifera visits differed relative to other visitors ($F_{1,138} = 8.9, P = 0.0035$). However, there was no interaction between floral display and visitor type ($F_{1,138} = 1.1, P = 0.2995$), indicating no difference between *A. mellifera* and others in the rate at which visitation changes with floral display. Interestingly, other insects very rarely attained the high visitation of *A. mellifera*.

Potential for Geitonogamy. The percent of bouts (sequence of flower visits among many plants by a single flower visitor) that contained intra-inflorescence floral visits did not seem to differ among six major *T. laxa* flower visitors (percent intra-inflorescence visits, number of bouts): *B.p. hirsuta* (22%, 9), *Autographa californica* (21%, 14), *A. mellifera* (20%, 379), *Bombus vosnesenskii* (20%, 10), *Sphaerophoria* sp. (17%, 6), and *Scaeva pyrastris* (14%, 7). However, plants that received intra-inflorescence visits ($N = 30$; mean = 2.76; 95% CI = 2.43–3.10; median = 3.0) had significantly more flowers per plant ($\chi^2 = 9.04, P = 0.0026$) than those plants that did not receive intra-inflorescence visits ($N = 186$; mean = 2.17; 95% CI = 2.04–2.31; median = 2.0).

Flower Visitor Quality. The quality of pollinator is often related to its ability to effect plant reproduction, but good substitute measures are time spent moving among and within flowers and plants. *A. mellifera*

visited significantly fewer flowers per minute than did *B.p. hirsuta* (Table 3). *A. mellifera* also spent significantly more time in flowers and between flowers than did *B.p. hirsuta*. Average number of flowers visited per plant did not differ significantly between the two species. *A. mellifera* was more variable in handling time and flight time than *B.p. hirsuta*. Visitation by *Papilio* was similar to that of *B.p. hirsuta*, and *Osmia* visitation was intermediate between *A. mellifera* and *B.p. hirsuta*.

Flower Visitation in Relation to Seed Set. In the absence of direct measurement of flower visitor effects on plant reproduction, insight can be gained through correlative evidence. As we measured flower visitation and plant reproduction in the same patches of *T. laxa* at both Vina and Park, flower visitation and plant reproduction can be visually contrasted. The mean number of visits to observation plots was significantly greater at Vina than at Park in both 2003 and 2005 (Fig. 4A); the difference, however, was much less in 2005. Percent seed set was significantly greater at Vina than at Park in 2003 but was not different between sites in 2005 (Fig. 4B). The greater difference in number of visits between sites in 2003 versus 2005 parallels the difference in percent seed set in 2003 versus 2005, suggesting a role of flower visitation in the percent of seeds matured. In addition, because almost all flower visits to observation plots were by *A. mellifera* (Fig. 1C), we can attribute the relationship between visitation and seed set largely to *A. mellifera*.

Discussion

Observations of visitors to flowers of *T. laxa* in observation plots and in transects showed a disproportionate abundance of *A. mellifera* relative to other (native) flower visitors. Despite mean visits to individual flowers not differing between *A. mellifera* and other flower visitors (Fig. 1B), absolute abundance of *A. mellifera* was far greater (Tables 1 and 2; Fig. 1A and C). The difference in abundance between *A. mellifera* and other flower visitors differed between sites (Table 2; Fig. 2), with Vina having higher *A. mellifera* abundance relative to other flower visitors. *A. mellifera* abundance may have varied between Park and Vina

Table 3. Contrast of quality components of *T. laxa* flower visitors

Variable	<i>Osmia</i> sp. (Megachilidae; Hymenoptera)	<i>Papilio glaucus</i> <i>rutulus</i> (Papilionidae; Lepidoptera)	<i>Apis mellifera</i> (Apidae; Hymenoptera)	<i>Battus philenor</i> <i>hirsuta</i> (Papilionidae; Lepidoptera)	<i>Apis mellifera</i> versus <i>Battus philenor hirsuta</i> ^a		
					df	t	P
N	3	2	15	13	—	—	—
Total observation time (min)	7.4	4.6	52.8	28.5	—	—	—
Visitation rate (flowers/min)	4.7 ± 0.6	7.6 ± 0.2	3.8 ± 0.4	7.5 ± 0.5	26	-5.7	<0.0001
Handling time (s)	7.7 ± 0.7	5.4 ± 0.3	10.4 ± 1.3	5.0 ± 0.7	26	4.0	0.0005
Flight time (s)	6.0 ± 1.0	2.7 ± 0.0	7.7 ± 1.1	3.9 ± 0.3	26	4.1	0.0004
Flowers visited per plant	1.2 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	1.3 ± 0.1	26	-2.0	0.0584

Values are means ± SE except for total observation time. Although some variables were transformed for analyses, untransformed values are shown here.

^a Results of two-sample *t*-tests (*A. mellifera* versus *B.p. hirsuta*) are shown for the four variables.

Handling time, time from initial contact with flower to departure; flight time, time spent flying between subsequent plants.

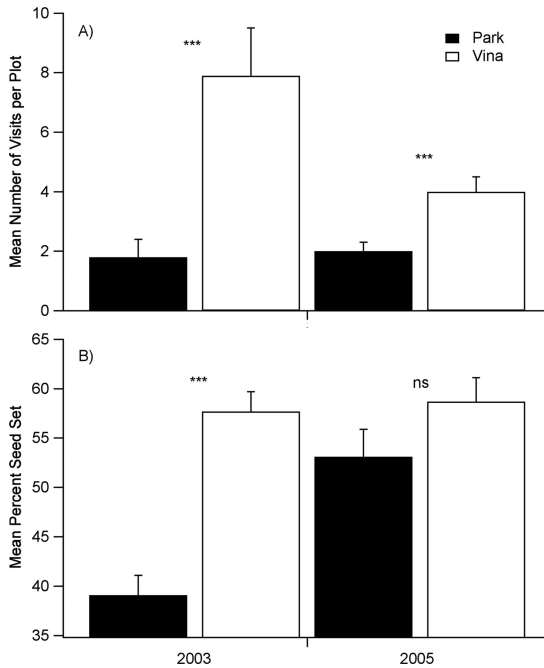


Fig. 4. Representation of *T. laxa* visitation in relation to percent seed set at Park and Vina for 2 yr. (A) Mean (\pm SE) visits per plot (N, number of plots: 2003, Vina [18], Park [18]; 2005, Vina [102], Park [138]); nonparametric two-sample Wilcoxon tests were used. (B) Mean (\pm SE) percent seed set (N, number of fruits: 2003, Vina [98], Park [102]; 2005, Vina [47], Park [48]); parametric two-sample *t*-tests were used. *** $P < 0.001$; ns, not significant.

through the effects of proximity to agriculture and/or feral colonies. Three studies reported honey bees foraging on average 1.7, 5.5, and 1.5 km from the nest (Visscher and Seeley 1982, Beekman and Ratnieks 2000, Steffan-Dewenter and Kuhn 2003). The distance of managed honey bees to our Vina site is well within this range. Although Park is much farther removed from agriculture, feral honey bee colonies exist nearby. In addition to distance to managed honey bees, honey bee abundance is higher near agriculture, as reflected in this study.

After *A. mellifera*, the next most abundant flower visitor (*B.p. hirsuta*) likely varies in importance for *T. laxa* throughout the plant's range through availability of its larval host plant (*Aristolochia californica* Torrey, [Aristolochiaceae]; Gilbert and Singer 1975). The Park site is a blue oak savanna, bordering a riparian corridor in a canyon that hosts an abundant source of *A. californica*. The greater distance to the corridor at Vina may be responsible for the lower abundance of *B.p. hirsuta* at Vina. The effects of lower abundance of butterflies on pollination rates may be counteracted to some extent by their ability to carry pollen longer distances relative to bees and flies (Courtney et al. 1982). In *Lavandula latifolia* Medicus (Lamiaceae), lepidopterans visit flowers more frequently and fly farther than bees and therefore are more likely to facilitate meta-population dynamics (Herrera 1989).

This could be especially important in *T. laxa*, whose seeds likely experience little long distance dispersal. Thus, *B.p. hirsuta*'s role in *T. laxa* pollination likely varies with co-occurrence of *T. laxa* and *A. californica*.

In addition to the importance of the abundance of flower visitors is the quality of their visits. *A. mellifera* visited fewer flowers per minute and spent more time in flowers, than did *B.p. hirsuta* (Table 3). Based on this evidence, *B.p. hirsuta* seems to be a "better" pollinator of *T. laxa* than *A. mellifera* because *B.p. hirsuta* potentially pollinated more flowers per minute and was perhaps less likely to cause self pollinations (but see below). Indeed, many studies have shown that flowering visits by *A. mellifera* cause more self-pollination than do native pollinators (Enyard and Galetto 2002, Hansen et al. 2002, Dick et al. 2003, Dupont et al. 2004). *B.p. hirsuta* did visit slightly more flowers per plant than did *A. mellifera*, but the difference was only just significant (Table 3). If *A. mellifera* visitation increases geitonogamy, *A. mellifera* would have had deleterious effects on *T. laxa* pollination because geitonogamy produces nearly zero seed set in *T. laxa* (Schlising and Chamberlain 2006). These results are inconsistent with those of Gross (2001), who found that *A. mellifera* visited more flowers per minute and spent less time in flowers than native pollinators.

Floral display often mediates plant-pollinator interactions and may influence the effect that *A. mellifera* has on plant species. One consequence of floral display size is that larger floral displays attract more flower visitors (Fig. 3). However, larger floral display also increases the number of flowers visited per plant and may result in geitonogamous self-pollination and stigma clogging in many plants (Ohashi and Yahara 2001, Harder and Barrett 1995, de Jong et al. 1993). If invasive pollinator species respond differently to floral display size than do native species, the consequences of floral display size for plants may change in the presence of invasive pollinators. In this study, although the magnitude of flower visitation as a function of floral display was greater for *A. mellifera* than for all other flower visitors (Fig. 3), *A. mellifera* did not respond to floral display differently (i.e., slopes were not different) from that of native flower visitors (Fig. 3). These results are consistent with those of prior studies that found no difference among *A. mellifera* and other pollinators in response to floral display (Robertson and MacNair 1995, Totland and Matthews 1998).

The total effect of flower visitors on plant reproduction has recently been shown to be closely related to interaction frequency (e.g., how many times bee species A visits an individual of plant species Z, per observation period; Vázquez et al. 2005). Specifically, as interaction frequency increases, the total effect tends to increase, regardless of interaction quality (e.g., pollen deposition). *A. mellifera* were far more abundant than other flower visitors in this study, suggesting that, if the relationship that Vázquez et al. showed holds here, *A. mellifera* delivers the largest pollination benefit to *T. laxa*. Given current information regarding frequency of interaction, *A. mellifera*

are strong interactors with *T. laxa*, whereas *B.p. hirsuta* are relatively weak interactors. Although we did not measure plant reproductive response to specific pollinators in this study, results from a previous study on *T. laxa* are informative. Although *T. laxa* produced more flowers and fruits per plant and more ovules per ovary, in each of two years at Park relative to Vina (Schlising and Chamberlain 2006), percent seed set was significantly higher at Vina in 2003, and higher, but not significantly so, in 2005 (Fig. 4). Higher flower visitation (Fig. 4), caused largely by *A. mellifera* (Figs. 1 and 2), is consistent with the difference in seed set. The foregoing discussion is largely conjecture, but data presented in Fig. 4 are highly suggestive.

Under what circumstances might *A. mellifera* be an important pollinator of other native plants? First, ruderal native plants primarily associated with agricultural settings may particularly benefit from *A. mellifera*. Second, native plants near feral colonies may benefit from *A. mellifera* but to a lesser extent than native plants near agriculture. Third, native plants with few native pollinators may greatly benefit from *A. mellifera* given native pollinator decline (Buchmann and Nabhan 1995). Fourth, because *A. mellifera* colonies persist longer than most native bee species, *A. mellifera* may be a more reliable pollinator throughout a season than species that have shorter activity periods. Last, *A. mellifera* are simply more abundant than their native relatives, such that they may be the most frequent interactors with many plant species. However, does the "predictable unpredictability" of *A. mellifera* behavior make their pollination services inferior to those of native bees (Westerkamp 1991)? The issue remains to be resolved.

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References Cited

- Barthell, J. F., J. M. Randall, R. W. Thorp, and A. M. Wenner. 2001. Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. *Ecol. Appl.* 11: 1870–1883.
- Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38: 567–593.
- Beekman, M., and F.L.W. Ratnieks. 2000. Long-range foraging by the honey-bee, *Apis mellifera* L. *Funct. Ecol.* 14: 490–496.
- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature (Lond.)* 398: 330–334.
- Buchmann, S. L., and G. P. Nabhan. 1995. *The forgotten pollinators*. Island Press, Washington, DC.
- Butz Huryn, V. M. 1997. Ecological impacts of introduced honey bees. *Q. Rev. Biol.* 72: 275–297.
- Committee on the Status of Pollinators in North America, National Research Council. 2007. *Status of pollinators in North America*. National Academies Press, Washington, DC.
- Courtney, S. P., C. J. Hill, and A. Westerman. 1982. Pollen carried for long periods by butterflies. *Oikos* 38: 260–263.
- de Jong, T. J., N. M. Waser, and P.G.L. Klinkhamer. 1993. Geitonogamy: the neglected side of selfing. *Trends Ecol. Evol.* 8: 321–325.
- Dick, C. W., G. Etchelecu, and F. Austerlitz. 2003. Pollen dispersal of tropical trees (*Dinizia excelsa*: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest. *Mol. Ecol.* 12: 753–764.
- Dicks, L. V., S. A. Corbet, and R. F. Pywell. 2002. Compartmentalization in plant-insect flower visitor webs. *J. Anim. Ecol.* 71: 32–43.
- Dupont, Y. L., D. M. Hansen, A. Valido, and J. M. Olesen. 2004. Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biol. Conserv.* 118: 301–311.
- Enyard, C., and L. Galetto. 2002. Pollination ecology of *Geoffroea decorticans* (Fabaceae) in central Argentine dry forest. *J. Arid Environ.* 51: 79–88.
- Gilbert, L. E., and M. C. Singer. 1975. Butterfly ecology. *Annu. Rev. Ecol. Syst.* 6: 365–397.
- Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 34: 1–26.
- Gross, C. L. 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biol. Conserv.* 102: 89–95.
- Gross, C. L., and D. Mackay. 1998. Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biol. Conserv.* 86: 169–178.
- Hansen, D. M., J. M. Olesen, and C. G. Jones. 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? *J. Biogeogr.* 29: 721–734.
- Harder, L. D., and S.C.H. Barrett. 1995. Mating costs of large floral displays in hermaphrodite plants. *Nature (Lond.)* 373: 512–515.
- Herrera, C. M. 1987. Components of pollinator "quality": comparative analysis of a diverse insect assemblage. *Oikos* 50: 79–90.
- Herrera, C. M. 1989. Pollinator abundance, morphology, and flower visitation rate: analysis of the "quantity" component in a plant-pollinator system. *Oecologia (Berl.)* 80: 241–248.
- Hickman, J. C. (ed.). 1993. *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley, CA.
- Hurd, P. D., Jr. 1955. *The carpenter bees of California (Hymenoptera: Apoidea)*. University of California Press, Berkeley, CA.
- Hurd, P. D., Jr., and C. D. Michener. 1955. *The megachilid bees of California (Hymenoptera: Megachilidae)*. University of California Press, Berkeley, CA.
- Kenta, T., N. Inari, T. Nagamitsu, K. Goka, and T. Hiura. 2007. Commercialized European bumblebee can cause pollination disturbance: an experiment on seven native plant species in Japan. *Biol. Conserv.* 134: 298–309.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10: 689–710.
- Michener, C. D. 2000. *The bees of the world*. John Hopkins University Press, Baltimore, MD.

- Moritz, R.F.A., S. Härtel, and P. Neumann. 2005. Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Ecoscience* 12: 289–301.
- Morse, R. A., and N. W. Calderone. 2000. The value of honey bees as pollinators of U.S. crops in 2000. *Bee Culture* 128: 1–15.
- [NOAA] National Oceanic and Atmospheric Administration. 2005. NOAA satellite and information service. (<http://www5.ncdc.noaa.gov/pdfs/cd/california>).
- Ohashi, K., and T. Yahara. 2001. Behavioural responses of pollinators to variation in floral display size and their influence on the evolution of floral traits, pp. 274–296. *In* L. Chittka and J. T. Thomson (eds.), *Cognitive ecology of pollination*. Cambridge University Press, Cambridge, United Kingdom.
- Paini, D. R. 2004. Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: a review. *Austral. Ecol.* 29: 399–407.
- Robertson, A. W., and M. R. MacNair. 1995. The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*. *Oikos* 72: 106–114.
- Roubik, D. W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201: 1030–1032.
- SAS Institute. 2004. JMP version 5.1.2. SAS Institute, Cary, NC.
- Schlising, R. A., and S. A. Chamberlain. 2006. Biology of the geophytic lily, *Triteleia laxa* (Themidaceae), in grasslands of the Northern Sacramento Valley. *Madroño* 53: 321–341.
- Simpson, S. R., C. L. Gross, and W. Silberbauer. 2005. Broom and honeybees in Australia: an alien liaison. *Plant Biol.* 7: 541–548.
- Steffan-Dewenter, I., and A. Kuhn. 2003. Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. B. Biol. Sci.* 270: 569–575.
- Thorp, R. W., D. S. Horning, Jr., and L. L. Dunning. 1983. Bumble bees and cuckoo bumble bees of California. *Bull. Calif. Insect Surv.* 23: 1–79.
- Totland, O., and I. Matthews. 1998. Determinants of pollinator activity and flower preference in the early spring blooming *Crocus vernus*. *Acta Oecol.* 19: 155–165.
- Traveset, A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* 21: 208–216.
- Vázquez, D. P., W. F. Morris, and P. Jordano. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8: 1088–1094.
- Visscher, P. K., and T. D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63: 1790–1801.
- Vockeroth, J. R., and F. C. Thompson. 1987. Family Syrphidae, pp. 713–743. *In* J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood (eds.), *Manual of Nearctic Diptera*, vol. 1 and 2. Research Branch, Agriculture Canada, Ottawa.
- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060.
- Westerkamp, C. 1991. Honeybees are poor pollinators—why? *Plant Syst. Evol.* 177: 71–75.

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