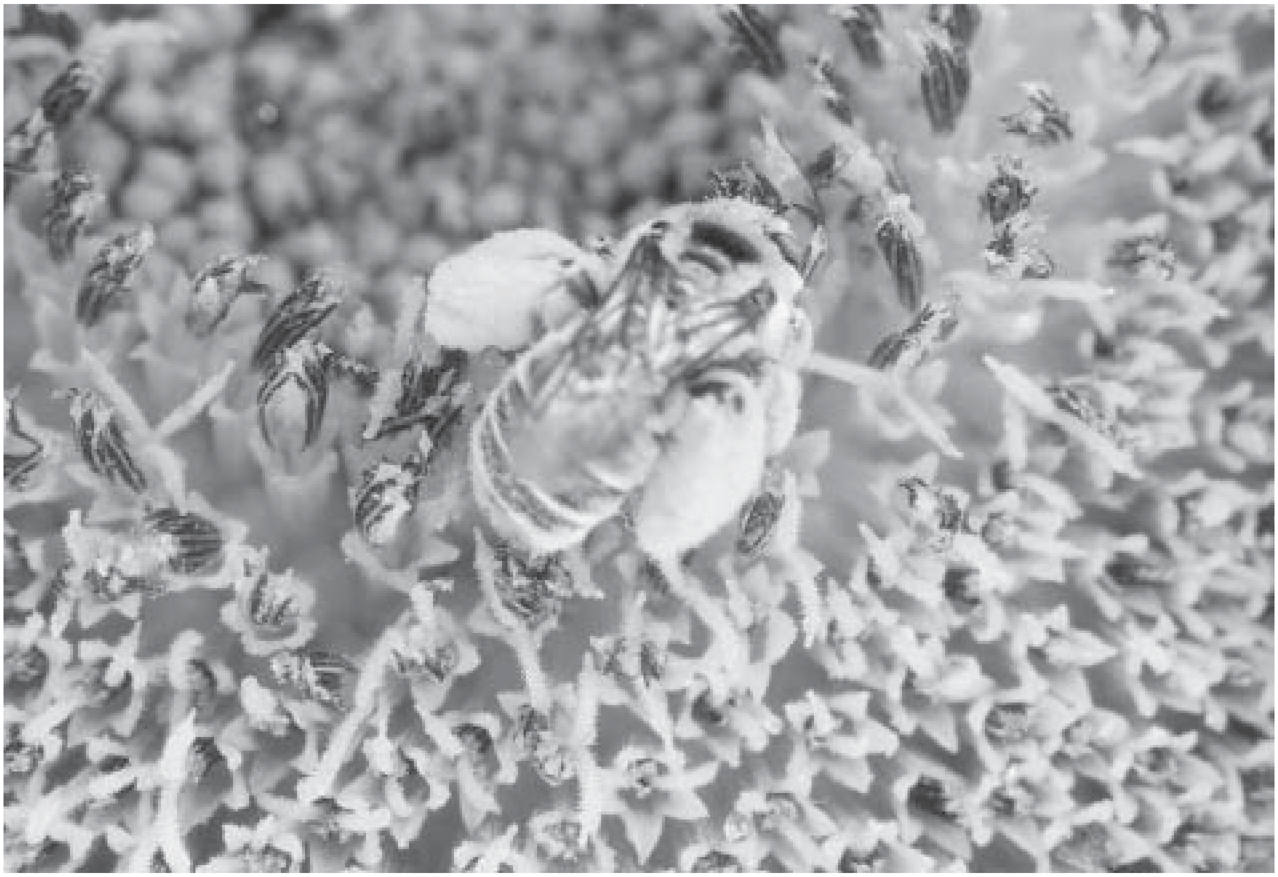

Diadasia, **the sunflower bee, on** *Helianthus annuus*. **Photograph by D.L. Briggs.**

NATIVE BEES, NATIVE PLANTS, AND CROP POLLINATION IN CALIFORNIA

by Claire Kremen, Robert L. Bugg, Nikki Nicola, Sarah A. Smith, Robbin W. Thorp, and Neal M. Williams

California is recognized globally as an area of exceptional plant diversity containing a host of plants found nowhere else in the world. It is also the most important agricultural area in North America, producing half of the US supply of fruits, nuts, and vegetables at an annual value of $16.45 billion, and exporting $6.5 billion of food and agricultural commodities abroad.

Insect pollinators are critically important both for the maintenance of California's diverse natural ecosystems and for its agricultural productivity. In 1997, honey bees alone were credited with contributing $4.2 billion to crop productivity in California (E. Mussen, pers. comm.). Here we focus on the under-appreciated role that native bees play in California's agricultural productivity, and how California's native plants support these native bee populations.

A large number of flowering plants (Angiosperms) rely on an animal for pollination, successful seed set, and fruit growth. Even self-fertile plants (e.g., tomatoes) or plants

Osmia lignaria, **the blue orchard bee, on almond. Photograph by D.L. Briggs.**

The Cache Creek Valley, showing large areas of chaparral-oak woodland adjacent to farm fields. Photograph by C. Kremen.

that are typically wind-pollinated (e.g., grapes) can benefit from animal "vectors"—animals that help to transport pollen. Their help makes possible cross-pollination, which can produce larger, better-tasting fruits with more viable seeds, and enhanced genetic diversity in seedlings.

In the United States, over 100 crops are bee-pollinated, and 15–30% of the average American diet is comprised of bee-pollinated foods. Thus, bee-pollinated crops make up an important component of human dietary stability and diversity. Some of the fruits and vegetables requiring bee pollination include: alfalfa, almond, apple, avocado, cantaloupe, cucumber, kiwi, plum, squash, sunflower, watermelon, and selected cultivars of apricot, citrus, peach, and strawberry. In addition, a far larger set of fruits and vegetables require insect pollinators for seed or hybrid seed production.

Bees (superfamily Apoidea) are thought to be the most important group of pollinators for both crop and non-crop plants. Female bees are one of the few insect groups that specialize in pollen collection to feed their larvae. Over time, they have developed physical traits designed for collecting pollen. These include numerous "hairs" on their bodies to which pollens adhere, and specialized structures known as scopae or corbiculae for storing and transporting pollen on their legs or abdomens.

Bees also tend to forage consistently on one plant species before returning to the nest to deposit their pollen loads. This behavioral fidelity enhances the chance that pollen will be transported from flower to flower of the same species, ensuring reproduction. Although male bees do not collect pollen, they too are often hairy and can transfer pollen as they visit flowers in search of nectar or mates.

Over 4,000 species of bees occur in North America, and 1,500 are currently found in California (Thorp, observations). The vast majority of these bees are "solitary" species rather than the familiar social honey bees and bumble bees. Females of solitary species collect pollen, mold it into a pollen "loaf," and seal it along with a single egg into a nest cavity.

Within this nest the larvae then hatch, complete development, and pupate, finally emerging as adults. All of this occurs with no further maternal care. Each bee species is specific in its choice of nesting substrate: these range from simple to elaborate tunnels dug into the ground, to cavities in twigs or dead wood.

Many farmers import colonies of the European honey bee, *Apis* *mellifera*, to ensure adequate pollination of crops requiring bee visits for fruit set. Unfortunately, declines in the availability of colonies due to diseases, loss of bee-keeping subsidies, and pesticides, have led to shortages of pollination services at times. Overall, there are now less than half the number of bee colonies that existed back in the 1950s, although the demand for bees in some areas continues to increase.

California uses over a third of the available 2.6 million commercial hives each year for almond pollination alone, importing many hives from other states as distant as the Dakotas, Texas, and Florida (E. Mussen, pers. comm.).

Native bee pollinators may be taking up some of the slack caused by honey bee shortages, but the quantitative importance of most native bee species in crop pollination remains largely undocumented. In a few cases, native bees are known to be more effective pollinators than honey bees. Examples include the alkali bee (*Nomia melanderi*) on alfalfa; bumble bee species on watermelon and blueberry; and various native bees on sunflower.

Native bees may be at risk, however, from environmental change. Pesticides have taken their toll on native bee populations as they have on honey bees, and have been responsible for the failure of the blueberry crop in Canada. Habitat loss, fragmentation, and degradation are suspected agents in the decline of native bee populations and diversity. Native bees require natural habitat to provide blooming plants throughout their flight period, and nesting sites for rearing young. As natural habitats are converted to industrial or agricultural uses, available areas that can support bees are declining.

Thus while natural ecosystems may be providing pollinators—and hence pollination services—for free, non-sustainable land use is potentially eroding these benefits. We therefore set out to understand the role of unmanaged native bees in crop pollination, and how the services they provide change as environmental conditions are altered. Since 1999 we have carried out this work in California in Yolo, Solano, and Napa counties; on farm sites situated in the Central Valley; and in the Cache and Putah Creek watersheds on the eastern edge of the Inner Coast Range.

ROLE OF NATIVE BEES IN CROP POLLINATION

To date, we have identified 65 native bee species that visit and potentially pollinate a variety of principally summer California crops, and 14 additional bee species that visit crops but probably do not contribute to pollination (see Table 1 on page 44). The latter species are either parasitic "cuckoo bees" that do not collect pollen themselves, or are bees that carry pollen internally.

Further investigation of spring crops (mostly orchards) will undoubtedly increase the number of species involved. For crops that we have investigated in detail, we found that native bees often make up a high proportion of the total bee visits (i.e., visits that include honey bees), suggesting that native bees can be as or more important than managed honey bees for these crops (Table 1).

In watermelon, a crop that requires multiple bee visits and deposition of 500–1,000 pollen grains for production of a marketable fruit, we found that the native bee community alone could provide sufficient pollination for the crop. This ability, however, depended on the diversity and abundance of bees in the community, which in turn was dependent on the abundance of native habitat in the area.

As agricultural operations have

A typical conventional farm field in the Sacramento Valley. No floral resources, other than those provided by the crop (in this case watermelon) are available. Photograph by C. Kremen.

expanded and intensified in areas of California, native habitat declined and could no longer support a sizeable native bee community. Consequently, native bees could no longer provide the needed pollination services without the addition of honey bee colonies.

The majority of organically-managed farms located near native habitat obtained sufficient pollination solely from the native bee community. For those located far from native habitat, a much smaller percentage of organically-managed farms and no conventionally-managed farms received sufficient pollination from native bees. These latter farms relied on honey bees for pollination.

We also found that crops typically thought of as "self-pollinated" benefited substantially from native bee visitation. Tomato flowers produce no nectar, and their pollen can only be accessed from poricidal anthers by high frequency vibration. Honey bees are unable to vibrate the flowers, and thus obtain few rewards from tomato flowers (hence the low proportion of honey bee visits, as shown in Table 1). However, bumble bees and other bees (e.g., *Anthophora urbana*) can obtain the pollen through vibration, and can often be found exploiting this honey bee-free niche.

By excluding bees from certain flowers, cross- and self-pollinating other flowers by hand, and then comparing these against flowers accessible to bees, Smith and Kremen (in prep.) found that native bees significantly increase the fruit set and size of Sungold cherry tomatoes by promoting cross-pollination.

TABLE 1. NUMBERS OF NATIVE BEE SPECIES AND PROPORTIONS OF TOTAL NATIVE BEE VISITORS (out of all bee visits including honey bees) to selected crops in Yolo and Solano counties, California

Crop	Native bee visitors (number of species)	Additional non-pollinating visitors (number of species)	Average proportion of total bee visits from native bees	Range across farms (proportions)
Watermelon	30	9	0.27	0.0 – 0.88
Sunflower	25	2	0.37	0.01 – 0.99
Strawberry	16	2	0.96	0.87 – 1.00
Muskmelon	11	0	0.08	0.0 – 0.42
Tomato	6	0	0.98	0.89 – 1.00
Almond	5	1	–	–
Eggplant	5	0	0.74	0.33 – 1.00
Cucumber	3	0	–	–
Squash	2	0	–	–
Total	**65**	**14**		

WILD HABITAT AND CROP POLLINATION

Many native bee species require a diversity of floral resources to provide nectar and pollen throughout their flight season. In addition, they require protected areas for nesting, including twigs, dead wood, bare soil, and abandoned rodent nests. It therefore seemed that native bee crop pollinators would more likely be found on farms close to natural habitat.

In order to test this hypothesis, we conducted two types of studies. First we measured the diversity and abundance of crop visitors to watermelons and tomatoes on farms that varied in nearby natural habitat from 0-80% cover within a 1 kilometer radius. For watermelon crop visitors, nearby natural habitat strongly affected both native bee diversity and total abundance. For tomato, which has only two types of frequent visitors, bumble bees (*Bombus* spp.) and *Anthophora urbana*, we found that the amount of natural habitat positively affected visitation by bumble bees but not by *A. urbana*.

Bumble bees nest in abandoned rodent nests and have long flight seasons, extending from early spring to late summer. In addition, bumble bee colonies produce only one reproductive generation per year, and thus only one nest is established per colony per season. Solitary *A. urbana* females excavate nests in the ground; this species has a shorter flight season from late spring to late summer. It is multivoltine (multiple reproductive generations per year), and nest sites could therefore shift over time to track the available floral resources from place to place.

Perhaps bumble bee queens seek out nest sites close to abundant floral resources in the early spring, which are largely concentrated in wild habitat. Later in the summer when most California wildland species have finished blooming, bumble bee workers forage at floral resources

Riparian habitat including *Cercis occidentalis* (western redbud), an important spring resource for bumble bees and other bees. Photograph by C. Kremen.

on farms, but are constrained to foraging within a certain distance of their nest sites in the wildlands.

In contrast, both farm and wild resources are abundant when *A. urbana* begins nesting, so females can choose either area for nesting. In addition, subsequent generations of *A. urbana* may shift nest sites to track resource availability and gradually move nest sites into agricultural areas.

We also surveyed bees in wild habitats in the Cache and Putah Creek watersheds in order to determine which of our crop pollinators also occur in the wild areas. These sites were characterized as either riparian or mixed chaparral and oak woodland. In fact, we found all of them there—54% in both habitat types, 17% in riparian alone, and 29% in chaparral/oak woodland alone.

CALIFORNIA NATIVE PLANTS AND BEES

Finally, we explored the habitat relationships and resource needs of bee species by sampling bees on California native plants in six chaparral/oak woodland and riparian sites from January through October of 2001. Our main focus was on perennials, shrubs, and trees. We now have detailed records of which native bee species utilize which plant species in this area. We are currently complementing the work presented here with a more comprehensive study that also includes native annuals, weeds, and crops monitored at biweekly intervals at 22 farms and natural area sites.

The results for the 2001 study are summarized in Table 2 (on pages 46 and 47). Table 2 shows which California perennials provide resources for the greatest number of important crop pollinator species. Importance of crop pollinator species was defined as those insects

TABLE 2. CROP AND NON-CROP VISITORS TO CALIFORNIA NATIVE PERENNIALS. Organized by the maximum number of important crop visitors (see text) visiting a plant. Species currently used in hedgerow or tail water plantings in Yolo and Solano counties are indicated by "Y"; other species available in nurseries are indicated by a *. A + indicates that European honey bees (*Apis mellifera*) were also observed foraging on these plants.

		Number of bee species				
Plant species	**Currently used in hedgerow or tailwater plantings**	**Important crop visitors**	**Other crop visitors**	**Parasitic bee crop visitors**	**Non-crop visiting bees**	**All bees**
Heteromeles arbutifolia+	Y	10	8	1	20	39
Eriogonum fasciculatum	Y	8	8	4	11	31
Baccharis salicifolia+	Y	5	8	0	19	32
Mentzelia laevicaulis+	–	5	2	0	1	8
Eriodictyon californicum+	–	4	4	1	26	35
Cercis occidentalis+	Y	4	9	1	10	21
Rosa californica+	Y	4	1	1	0	6
Lotus scoparius+	–	3	3	0	15	21
Adenostoma fasciculatum+	*	3	7	1	3	14
Lupinus succulentus+	–	3	1	0	3	6
Cornus sericea+	*	3	3	0	1	6
Eremocarpus setigerus	–	3	1	1	1	6
Eriophyllum lanatum	–	2	2	0	8	12
Baccharis pilularis+	Y	2	4	0	6	12
Hemizonia congesta	–	2	0	0	1	3
Lupinus microcarpus	–	2	0	0	1	2
Ceanothus cuneatus+	Y	1	8	0	11	20
Lepechinia calycina+	–	1	4	1	10	16
Epilobium canum+	*	1	4	0	4	9
Stephanomeria virgata	–	1	1	0	4	6
Salix laevigata+	Y	1	4	0	2	7
Mimulus aurantiacus+	Y	1	2	1	2	6
Rhamnus californica	Y	1	3	0	2	6

TABLE 2 (CONT.)

Plant species	Currently used in hedgerow or tailwater plantings	Number of bee species: Important crop visitors	Other crop visitors	Parasitic bee crop visitors	Non-crop visiting bees	All bees
Sambucus mexicanus+	Y	1	2	0	2	5
Madia elegans	–	1	0	0	1	2
Arctostaphylos manzanita+	Y	1	2	0	1	3
Rupertia physodes	–	0	0	0	7	7
Ceanothus oliganthus+	–	0	2	0	6	8
Salix sessilifolia	–	0	1	0	3	4
Wyethia helenioides+	–	0	1	0	3	4
Calystegia purpurata	–	0	3	0	2	5
Lupinus albifrons+	*	0	1	0	2	3
Fraxinus dipetala	–	0	0	0	2	2
Clarkia sp.	–	0	0	0	1	1
Phacelia imbricata	–	0	0	0	1	1
Toxicodendron diversilobum+	–	0	0	0	1	1
Triteleia laxa	–	0	0	0	1	1
Aesculus californica+	Y	0	1	0	0	1
Clematis lasiantha	*	0	1	0	0	1
Eriogonum nudum	–	0	1	0	0	1
Eschscholzia californica	Y	0	1	0	0	1
Total bee species in category		**16**	**49**	**14**	**113**	**192**

visiting three or more of the crops listed in Table 1. In total, we document records of 192 native bee species on 41 native plant species. Table 2 also lists the number of other crop visitors and of non-crop-visiting native bee species.

Many of the plant species important for the crop pollinators also provide resources for other bee species. Six of the 10 plant species with the greatest number of records for important crop pollinators were also critical for other bee species (*Eriodictyon californicum*, *Heteromeles arbutifolia*, *Baccharis salicifolia*, *Lotus scoparius*, *Eriogonum fasciculatum*, and *Cercis occidentalis*). The remaining top 10 plants for crop pollinators included *Mentzelia laevicaulis*, *Rosa californica*, *Adenostoma fasciculatum*, and *Cornus sericea*, and for non-crop visitors were *Ceanothus cuneatus*, *Lepechinia calycina*, *Eriophyllum lanatum*, and *Rupertia physodes*.

Since the honey bee, *Apis mellifera*, is also an important, although non-native, crop pollinator, Table 2 lists the native plants at which we observed *A. mellifera* foraging. This species makes use of a wide variety of the California flora, and beekeepers clearly benefit during off-crop seasons by using wild areas for bee forage.

CONCLUSIONS

Our work during the past four years has documented that California's native bees make an important contribution to crop pollination. This contribution could become even more valuable as an "insurance policy" if honey bees become more scarce or fail altogether. We have also shown that all of these native bee species occur in wild habitats and show some degree of dependence on the native California flora.

Finally, the destruction of native habitat in the Central Valley appears to be related to a decline in the diversity and abundance of native bees found there, along with a concomitant reduction in the crop pollination services they provide. A hopeful sign, however, is that even small fragments of wild or semi-wild habitat still sport diverse and abundant bee faunas, such as at the Cache Creek Nature Preserve, a 130-acre riparian and upland area that is currently being restored.

It is important to conserve bee habitat to maintain the valuable crop pollination services that bees provide. In Yolo, Solano, and Napa counties, certain areas are already protected to some degree, including, for example, the Cache Creek Nature Preserve, Jepson Prairie, Yolo Basin Wildlife Area, Putah Creek UC Davis Campus Reserve, Quail Ridge Reserve, Cold Creek Canyon Reserve, Cache Creek Canyon Regional Park, Nichols County Park, and the Bureau of Land Management lands along Blue Ridge. All but the first four sites, however, are located in the hilly areas of the Inner Coast Range, and very few natural or semi-natural lands remain within the Sacramento Valley itself.

Eriodictyon californicum (yerba santa) and _Mimulus aurantiacus_ (sticky monkeyflower) of chaparral. _E. californicum_ is visited by a wide number of bee species, whereas _M. aurantiacus_ is rarely visited, and only by a few species. Photograph by C. Kremen.

Bringing bees back to the Sacramento Valley would require an extensive restoration effort. Nonetheless, the dream of restoring healthy communities of pollinators by restoring their plant communities is not outside the realm of possibility. On-going restoration efforts along Cache Creek and Putah Creek can ultimately provide archipelagoes and corridors of bee-friendly habitat. Over the next 30 years, 1,000 acres of restoration efforts are planned along Cache Creek alone (J. Lowrey, pers. comm.).

Farmers can assist the restoration process and benefit their own crops through the planting of "insectary plants" that provide habitat and resources for beneficial insects ranging from predators to pollinators. The Community Alliance of Family Farmers and the Yolo County Resources Conservation District actively encourage the planting of hedgerows and tailwater ponds using native plants (including some of the plants listed in Table 2).

Many of the plants that farmers are already using were selected because they provide pollen or nectar to other beneficial insect species, primarily predators and parasitoids of crop pests. Our data show that many of these plants also benefit some of the most important crop pollinators, as well as other bee species.

Some potentially important plants for pollinators, however, are either difficult to include in hedgerow plantings because they cannot be brought into cultivation, such as *Eriodictyon californicum* (J. Gerland, pers. comm.) or have not yet been tested (e.g., *Lotus scoparius*). Some of these plants may prove critical—providing resources for a particularly important bee species, or filling in a "phenological window" during which no bee-attractive plants from the current hedgerow list are blooming.

Our current research will provide a rich dataset for identifying new plants to add to existing reserve and farm restoration efforts for the benefit of the pollinator community. And "bringing back the bees" will ensure a much rosier future for California's native flora.

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