POLLEN AND NECTAR RESOURCE OVERLAP AMONG BEES ON SANTA CRUZ ISLAND

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ABSTRACT

In 1988, we initiated studies on the potential impact of introduced feral European honey bees on native bees and pollination of flowering plants on Santa Cruz Island. Honey bees tend to forage most frequently on introduced flowering plants. Their food resource use overlaps primarily with generalist native bees. Results obtained provide a baseline to determine effects of removing honey bees on restoration of native bees and pollination systems. Removal of honey bees from this isolated ecosystem is nearly complete and is predicted to: 1) increase food availability for native bees; 2) reduce seed set of some introduced flowering plants; and 3) have little or no negative effect on seed production of most native plants, including rare and endemic species. Long-term monitoring of native bee populations and experiments on plant reproduction are being used to test these predictions. Complications include: 1) recent invasion and spread of an alien leafcutting bee that may become the important pollinator of yellow star-thistle; 2) some alien plants may be important food resources for some native bees; 3) removal of grazing animals; 4) extreme rainfall fluctuations from prolonged drought to El Niño induced wet; and 5) dramatic increases in some weeds, especially fennel.

Keywords: Honey bee, *Apis mellifera*, leafcutting bee, *Megachile apicalis*, native bees, resource overlap, pollination, bee diversity, ecosystem restoration, Santa Cruz Island.

INTRODUCTION

The honey bee, *Apis mellifera* L., and its many subspecies and races are native to much of Europe, Africa, and parts of Asia. It has been purposefully introduced from Europe to most of the world. In most countries where it has been introduced, concerns have been expressed by some that the honey bee may compete with native bees and other flower-visiting organisms for pollen and nectar resources, may interfere with effective pollination of native flora, may cause abnormal hybridization in some plants, and may compete with birds and mammals for nest cavities (Pyke and Balzer 1985; Willis et al. 1990; Paton 1993; Sugden et al. 1996; Butz Huryn 1997). Some tests have added and removed honey bee colonies and measured all bees before, during, and after these perturbations (Schaffer et al. 1979, 1983; Pyke and Balzer 1985). These perturbation experiments were limited to short-term measures and did not address potential long-term reproductive effects. Few studies have dealt with effects on reproductive biology of potential competitors (Roubik 1978, 1980, 1982, 1983, 1989, 1996a, 1996b; Roubik et al. 1986; Sugden and Pyke 1991; Paton 1993).

Santa Cruz Island provides a potential study site for testing long-term effects of removal of honey bees. It is far enough from the mainland (ca. 25 miles) to prohibit reestablishment on their own without aid of human transport. The bee fauna is relatively well known (Rust et al. 1985; Thorp et al. 1994). Procedures for removal of honey bees are discussed by Wenner and Thorp (1994) and Wenner et al. (1999, this volume). Background information on the biodiversity, resource use, and overlap of resource use between honey bees and other bees on Santa Cruz Island are discussed by Thorp et al. (1994). This paper updates results of our studies since 1993.

This paper represents the second part of the Santa Cruz Island bee saga. Wenner addressed the first part, the removal of European honey bees (Wenner and Thorp 1994; Wenner et al. 1999, this volume). The removal of honey bees from Santa Cruz Island is nearly complete (Wenner et al. 1999, this volume). This second part of the study considers the impact of honey bee removal on native bees and pollination systems of native and exotic flowering plants. In 1988, when Wenner and coworkers started dealing with the problem of European honey bee removal, we also initiated collection of baseline data on biodiversity of bees, flower visitation, and overlap in use of pollen and nectar resources between native and introduced bees (Thorp et al. 1994).

MATERIALS AND METHODS

Sampling of bees to determine faunal diversity, floral resource use and overlap, and reproductive biology included

the use of various "low technology" tools. The same was true for our gathering of data on visitation patterns, guilds of bee visitors, and their relative abundances at flowers. Aerial insect net collections and visual observations of bees at flowers provided the main sources of data. The latter included walking transects and stationary, timed counts at various flowers.

Trap-nests helped determine the reproduction of species of the guild of cavity-nesting bees (Thorp et al. 1992). This guild of bees was selected for ease of monitoring and comparison with similar data being gathered at several mainland sites in central California in another project being conducted in cooperation with Gordon Frankie, University of California, Berkeley (Thorp et al. 1992; Thorp 1996).

We have also collected some data on diversity of bees and their floral resource use from Santa Rosa Island. These data provide a baseline for comparison with the fauna and flora of an adjacent island off the coast of southern California that has never had honey bees.

Additions to the baseline data in Rust et al. (1985) and Thorp et al. (1994) are in Tables 1 through 4.

RESULTS

Since our initial publication (Thorp et al. 1994), we have accumulated additional records that can be added to Tables 1 and 3, and Appendices 1 through 3 of that paper. We have found an additional nine species of bees on the island (Table 1), all natives. We also add 13 more flowering plants used as food sources by honey bees (Table 2). Native bees visit a total of 11 of those 13 flowering plant species and share pollen and nectar resources of these plants with honey bees (Table 3). We also observed native bees visiting flowers of *Eucalyptus globulus* Labill and *Raphanus sativus* L., especially *Andrena prunorum* Cockerell on wild radish.

Among the endemic plants visited by honey bees, we have additional records of other bee visitors to *Lyonothamnus floribundus* A. Gray: *Andrena* sp., *Augochlorella pomoniella* Cockerell, *Ceratina acantha* Provancher, *Colletes* sp., *Hylaeus* sp., and *Protosmia rubifloris* (Cockerell). The overall guild of flower visitors also includes small wasps and beetles, especially tumble flower beetles (Mordellidae).

Additional plants monitored, but not visited by honey bees include: natives *Artemisia californica* Less. (coastal sagebrush), *Comarostaphylos diversifolia* (Parry) Greene (summer holly), *Helianthemum scoparium* Nutt. (common rush-rose), and *Sisyrinchium bellum* S. Watson (blue-eyed grass); endemics *Malacothamnus fasciculatus* (Torr. & A. Gray) Greene var. *nesioticus* (B. L. Rob.) Kearney (Santa Cruz Island bush mallow) and *Rhamnus pirifolia* Greene (island redberry); and alien: *Malva parvifolia* L. (cheeseweed). An endemic species of special interest that is not visited by honey bees is the Santa Cruz Island bush mallow, *Malacothamnus*. The guild of bee visitors observed at flowers of this plant include: *Augochlorella pomoniella*, *Bombus edwardsii* Cresson, *Ceratina acantha*, *Diadasia nitidifrons* Cockerell, *Dialictus* sp., *Halictus* (*Seladonia*) sp., *Lasioglossum channelense* McGinley, and *Osmia* sp., with most frequent visitation by *Ceratina* females and *Lasioglossum* males.

The introduced leafcutting bee, *Megachile* (*Eutricharaea*) *apicalis* Spinola has expanded its range on the island (Figure 1). During the drought years from 1988 through 1991, it seemed limited to the area of the University of California (UC) Field Station and Islay Canyon. In 1992,

Table 1. New species records and additions to biogeographic relationships and floral host specializations of bees found on Santa Cruz Island for 1994 to 1998[1].

Species	Distribution[2]	Flower Hosts
Andrenidae		
Andrena (*Diandrena*) *gnaphalii* (Cockerell)	SoCA	ligulate Asteraceae
Halictidae		
Halictus farinosus Smith	W USA	generalist
Lasioglossum titusi (Crawford)	Pac Coast	Asteraceae
Megachilidae		
Callanthidium illustre (Cresson)	W NA	generalist
Ashmeadiella opuntiae (Cockerell)	W NA	Cactaceae
Megachile angelarum Cockerell	W NA	generalist
Coelioxys octodentata Say	NA	generalist
Anthophoridae		
Diadasia nigrifrons (Cresson)	W USA	*Sidalcea*
Diadasia nitidifrons Cockerell	W USA	*Malacothamnus*[3]

[1] Additions to Tables 1 to 3 in Thorp et al. 1994.

[2] From Hurd 1979.

[3] On the mainland it occurs mostly on *Sphaeralcea*, but also known to visit *Malacothamnus*.

Table 2. Additional records of flowers visited by honey bees on Santa Cruz Island for 1994 to 1998.

Flowers	Status[4]	Preferred by *Apis*	Preferred for[5]	Visited by non-*Apis* bees
Eriophyllum confertiflorum (golden yarrow)[2]	N	N	+	+
Hedera helix (English ivy)	I	PN	+	-
Hirschfeldia incana (sort-podded mustard)[3]	I	PN	+++	+
Lathyrus vestitus (wild pea)[2]	N	N	+	+
Lupinus albifrons (silver lupine)[2]	N	P	+	+
Melilotus indicus (yellow sweet clover)[2]	I	N	+	+
Persea americana (avocado)	I	N	+	+
Raphanus sativus (wild radish)[2]	I	PN	+++	+
Rhus ovata (sugar bush)	N	PN	+	+
Rosmarinus officinalis (Rosemary)	I	N	+++	-
Stephanomeria exigua coronaria (milk-aster)	N	PN	+	+
Veronica anagalis-aquatica (water speedwell)[2]	I	PN	+	+
Wisteria sp. (wisteria)	I	N	+	+

[1] Additions to Appendix 1 in Thorp et al. 1999.

[2] Plant species formerly listed in Appendix 3 in Thorp et al. 1994 as not visited by *Apis*.

[3] Some records reported in Thorp et al. 1994 under *Brassica* sp. probably belong here.

[4] Status abbreviations: N = native; I = introduced.

[5] Used by *Apis* for: N = nectar; P = pollen; PN = both pollen and nectar.

it was found in the lower half of the Navy Road and by 1993 it had been found at the Chapel at the Main Ranch and as far west as Cascada. By 1994, it had reached the lower portion of Portezuela. By September 1996, it was found at Prisoners Harbor and to the west at the bottom of Centinela Grade. By October 1997, its range extended from the Main Ranch Airstrip to the Pozo drainage in the southwest of the island. This expansion has been in conjunction with the presence of its principle food host, yellow star-thistle, *Centaurea solstitialis* L. However we have also found females visiting flower heads of *C. mellitensis* L. to a lesser extent. In addition, we have records of one male each on *Marrubium*, *Silybum*, and *Grindelia*.

Cavity nesting species of bees that have occupied our trap-nests include: *Anthidium maculosum* Cresson, *Ashmeadiella opuntiae* (Cockerell), and *Megachile apicalis*. The most frequent occupations have been by *Anthidium*. In addition native spider wasps of the genus *Trypoxylon* and eumenid wasps of the genus *Euodynerus* compete with bees for nest holes. The European earwig, *Forficula auricularia* L., also competes with cavity-nesting bees and wasps for tunnels, especially in wet years.

Nest sites of numerous ground nesting species of bees have been located including: *Colletes* sp., *Andrena* (*Hesperandrena*) spp., *A.* (*Diandrena*) spp., *A.* (*Onagrandrena*) *oenotherae* Timberlake, *A.* (*Plastandrena*) *prunorum*, *A.* (*Tylandrena*) *subaustralis* Cockerell, *Agapostemon texanus* Cresson, *Anthophora edwardsii* Cresson, *Habropoda depressa* Fowler, and *H. miserabilis* (Cresson). We have also encountered the cuckoo bee, *Melecta separata callura* (Cockerell), and the nocturnal mutillid wasp, *Sphaeropthalma* sp. in association with nests of *Anthophora edwardsii*. One of us (AMW) found a huge nest site of *Andrena prunorum* in April 1998. Investigations into the nest biology of this bee were conducted in April and July by RWT. This bee is apparently bivoltine with overlapping generations, since both eggs and pupae were found in nests in April. Eggs to overwintering post-defecating larvae were found in July.

On 21 March 1994, AMW and assistants collected bees mostly on *Brassica* on the eastern end of Santa Cruz Island. These collections produced no honey bees, but yielded a total of 298 individuals belonging to 13 genera and over 20 species of native bees.

Counts of bees at flowers show that *Apis* declined sharply in conjunction with the heavy mortality caused by varroa mites (see Wenner et al. 1999, this volume). In the past one could be sure to see large numbers of honey bees at the more preferred flowers. During the past two years we have had to hunt diligently to find sites still supporting foraging honey bees. One of us (AMW) made collections in early September 1997 on four plant species (mustard, yellow star-thistle, coastal goldenbush, and island buckwheat) and early January 1998 on manzanita. In September 1997 a total of eight honey bees were found on mustard (four at two sites), and on yellow star-thistle (four at one site) while all four plant species yielded 8 genera, 11 species and 94 individuals (27 males, 57 females) of native bees. A survey of bees visiting manzanita in January 1998 (the same transect surveyed in January 1992) produced no honey bees, but did

Table 3. Additions to food resource sharing: flowers visited by honey bees and new records for the guilds of other bees that visit them on Santa Cruz Island for 1994 to 1998.[1]

Eriophyllum confertiflorum (golden yarrow)
Augochlorella pomoniella, *Colletes* sp., *Megachile* sp., *Melissodes* sp.

Eucalyptus globulus (blue gum)[2]
Agapostemon texanus, *Dialictus* sp. 1, *Dialictus* sp. 2.

Hirschfeldia incana (short-podded mustard)
Augochlorella pomoniella, *Colletes* sp., *Ceratina acantha*, *Melissodes* sp., *Triepeolus* sp.

Lupinus albifrons (silver lupine)
Anthidium maculosum, *Anthophora edwardsii*, *Bombus edwardsii*, *Diadasia bituberculata*, *Habropoda depressa*, *Megachile brevis*, *M. coquilletti*, *Synhalonia* sp.

Melilotus indicus (yellow sweet clover)
Andrena sp.

Persea americana (advocado)
Andrena prunorum, *Ceratina acantha*, *Evylaeus* sp., *Halictus* (*Seladonia*) sp., *Hylaeus* sp.

Raphanus sativus (wild radish)
Agapostemon texanus, *Andrena prunorum*, *Andrena* spp., *Anthophora edwardsii*, *Augochlorella pomoniella*, *Bombus edwardsii*, *Ceratina acantha*, *Dialictus* sp., *Evylaeus* sp., *Halictus* (*Seladonia*) sp., *Hylaeus* sp, *Lasioglossum channelense*, *Melecta separata callura*, *Nomada* sp, *Synhalonia* sp.

Rhus ovata (sugar bush)
Agpostemon texanus, *Andrena cerulea*, *Andrena* spp., *Bombus edwardsii*, *Evylaeus* sp., *Habropoda depressa*, *Hylaeus* sp., *Nomada* sp., *Protosmia rubifloris*.

Stephanomeria exigua coronaria (milk-aster)
Augochlorella pomoniella.

Veronica anagalis-aquatica (water speedwell)
Ceratina acantha.

Wisteria sp. (wisteria)
Bombus edwardsii.

[1]Additions to Appendix 2 in Thorp et al. 1994.
[2]On Appendix 1 list of flowers used by Apis in Thorp et al. 1994, but no other bees known as visitors at this time.

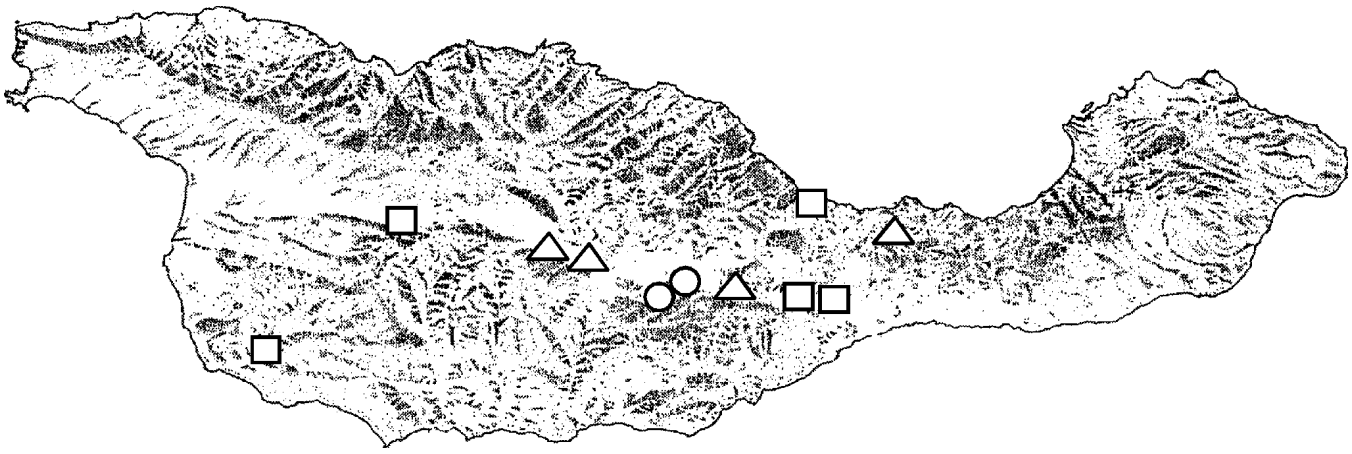

Figure 1. Santa Cruz Island: distribution of the introduced leafcutting bee, *Megachile apicalis,* since its first detection in 1988. Circles = 1988-1994; triangles = 1996; squares = 1997-1998.

yield native bees of 4 genera, 5 species and 18 individuals (6 males, 12 females). At the few remaining sites in the Central Valley where honey bees still forage we made a number of transect counts through yellow star-thistle in July 1998 (Table 4). In addition, we found three honey bees at the eastern Pine Forest in 10 minutes with three observers = 0.03 bees/observer minute and two honey bees in 35 minutes with one observer in lower Portezuela = 0.06 bees/observer minute druing our search from the eastern sheep fence to Christy Ranch in July 1998. Counts at yellow star-thistle in September 1998 produced a total of 83 bees in 41 minutes, only five were honey bees. There was also a diverse guild of non-bee visitors on yellow star-thistle in September 1998 including Lepidoptera (*Vanessa*, *Papilio*, *Pieris*, Hesperiidae, *Celerio lineata* (Fabricius), and Noctuidae); Diptera (*Eristalis*, Syrphidae, Bombyliidae), and Hymenoptera (*Bembix*).

Oligolectic bees often occur in association with plants rarely or never visited by *Apis* and may be their most important pollinators. Those bees include *Diadasia biturberculata* (Cresson) on *Calystegia*, *Diadasia nigrifrons* (Cresson) on *Sidalcea*, *D. nitidifrons* on *Malacothamnus*, *D. rinconis* Cockerell on *Opuntia*, *Andrena* (*Diandrena*) spp. on *Lasthenia*, *A.* (*Hesperandrena*) spp. on *Lasthenia*, and *A.* (*Onagrandrena*) *oenotherae* on *Camissonia*.

Table 4. Honey bee abundance on yellow star-thistle (*Centaurea solstitialis*) in the Central Valley of Santa Cruz Island in July 1998.

Day	Location	No. of *Apis*	Observation Period (min)	No. of Observers	No. of *Apis* per observed min.
20	E of Main Ranch	3	20	2	0.07
20	E of Main Ranch	3	20	2	0.07
20	Chapel	5	5	2	0.5
20	Main Ranch to Field Station	0	5	2	0
22	W of Sherwood E plot 1	17	20	2	0.43
22	W of Sherwood E plot 2	23	20	3	0.38
22	W of Sherwood E plot	7	20	3	0.12

SUMMARY AND DISCUSSION

Rust et al. (1985) published lists of bees known from the Channel Islands that included 84 species from Santa Cruz Island. We provided additions to these records (Thorp et al. 1994), raising the total number of bees reported for Santa Cruz Island to 105. Since 1993, we found an additional nine species of native bees on the island (Table 1). *Ashmeadiella* was reared from a trap-nest, *Callanthidium* and *Chalicodoma* are also known to nest in preexisting cavities, and *Coelioxys* is a cuckoo bee that lays its eggs in nests of *Megachile*. The other five species nest in the ground. Four of the species are pollen specialists (oligolectic bees). *Diadasia nitidifrons*, a pollen specialist on Malvaceae, was found visiting the endemic bush mallow, *Malacothamnus*, an association that also occurs at a mainland site, Mount Diablo State Park (RWT unpublished observation).

We found 13 more flowering plants used for food sources by honey bees since 1993 (Table 2). Five of these are natives; the other eight are introduced plants. Of the 13 additional species visited by honey bees, the most favored are introduced plants, including one for nectar only. Three of those introduced plants (*Hedera*, *Rosmarinus*, and *Wisteria*) do not appear in the Flora of Santa Cruz Island (Junak et al. 1995) because they have not escaped from plantings in association with the Main Ranch and the UC Field Station. Four of the native plant species are also visited by native bees and are only sparingly utilized by honey bees. The introduced wild radish is heavily visited by native bees, especially *Andrena prunorum*.

In an earlier paper (Thorp et al. 1994), we reported finding *Apis* on 57 of 154 (37%) flowering plants examined. In that paper introduced flowering species comprised about 35% of our honey bee visitation records, and most of the highly "preferred" floral resources were introduced species. With our new data these percentage figures increase slightly. Honey bees visited flowers of 70 of 168 (41.7%) of the flowering plants examined. Of those 70, 40.0% (28) are introduced species. Those 28 include most of the flowers on which we most frequently encounter foraging honey bees and overlap with native bees.

We continue to test our initial predictions that removal of honey bees from Santa Cruz Island should: 1) increase food availability for native bees, 2) reduce seed set of some introduced weedy flowering plants, and 3) have little or no negative impact on seed production of most native plants, including rare and endemic species (Thorp et al. 1994). Our approach is to use long-term monitoring of honey bee and native bee populations. Experiments on plant reproduction are being used or will be used to test these predictions (see Barthell et al. 1999, this volume).

In 1992, we monitored a transect along the South Ridge Road to determine the numbers of honey bees versus native bees visiting flowers of manzanita (Wenner and Thorp 1994). In January 1998, honey bees were absent along this transect due to depredations by varroa mites. The manzanita

supported a diverse assemblage of native bees. Their numbers were low, but this was probably due to the El Niño weather pattern that caused delays of two to four weeks in emergence of many native bees and other insects throughout California.

With the recent sharp decline in honey bees on the island (Wenner et al. 1999, this volume), foraging pressure on overlapping resource plants decreased, especially on introduced weeds. In September 1998 on yellow star-thistle, honey bees represented only 6% in contrast to 97% in July 1994 (Barthell et al. 1999, this volume). Nectar feeders other than bees were also frequently seen on yellow star-thistle, especially Lepidoptera and Diptera. Thus a more diverse total guild of flower feeders visits yellow star-thistle than indicated by our list of the guild of bees (Thorp et al. 1994).

Reduction in seed set after removal of honey bees may not occur as predicted for some other exotic weeds since they are also frequently visited by diverse guilds of native bees. Examples may include Asteraceae: *Centaurea solstitialis*, *Cichorium intybus* L., and *Silybum marianum* (L.) Gaertn.; Brassicaceae: *Raphanus sativus*, *Brassica* spp. and *Cakile maritima* Scop.; Fabaceae: *Lotus corniculatus* L.; and Lamiaceae: *Marrubium vulgare* L.. We have found that *Apis* contribute signigficantly to reproduction of yellow star-thistle, especially on the mainland and may have been responsible for its initial rapid spread (Barthell et al. 1994, 1995). However, the introduced leafcutting bee, *Megachile apicalis* continues to expand its range on Santa Cruz Island (Figure 1) and may perpetuate and enhance the reproduction of yellow star-thistle in the absence of the honey bee.

This is supported by many of our observations to date. Most of the native plants that honey bees seem to prefer also have diverse guilds of native bees or may be primarily pollinated by other insects (Thorp et al. 1994). *Asclepias fascicularis* Decne in A.DC. is frequently visited by a variety of wasps. *Baccharis salicifolia* (Ruiz & Pav.) Pers. (as *glutinosa* Pers.) has a diverse guild of bee visitors and is often visited by flies and other insects. *Prunus* and *Toxicodendron* are visited by numerous small native bees although the generic diversity is not great. *Heteromeles* frequently receives visits by a diverse assemblage of bees, and *Salvia* is heavily visited by numerous large bees.

Native gumplant, *Grindelia camporum* Greene, and yellow star-thistle have similar guilds of bee visitors (Thorp et al. 1994), but gumplant received a low preference rating for honey bee visits. We find that native bees are far more frequent visitors than honey bees to gumplant (Barthell et al. 1999, this volume). We have not found honey bees visiting the endemic *Malacothamnus*. Honey bees are mostly rare visitors compared to native bees and other insects at flowers of other island endemics: *Dudleya nesiotica* (Moran) Moran, *Lyonothamnus*, and *Malacothrix* (Thorp et al. 1994). Thus, removal of honey bees from the island will not likely have any detrimental impact on the reproduction of these species.

Many oligolectic (pollen specialist) bees tend to be dominant visitors to their host plants and are likely to be their most important pollinators. Honey bees rarely visit flowers of those plants on Santa Cruz Island. We recorded honey bees only rarely from *Calystegia* and not at all from *Camissonia*, *Lasthenia*, *Malacothamnus*, *Opuntia*, and *Sidalcea*.

This research project provides an unique opportunity to test effects of removal of *Apis* that is not feasible in most mainland sites. However, Santa Cruz Island has undergone many changes since just before and during the tenure of our studies (Thorp 1996). The effects of many of these, especially in combination, may overwhelm our abilities to sort out predicted changes that may be attributed to honey bee removal. Such changes include: 1) removal of sheep (by about 1987) and most of the cattle (by 1988); 2) weather-prolonged drought (1987-1990); 3) subsequent unusual spring rain patterns in 1990-1992 (1991 March miracle and 1992 February rains) followed by above normal rains during the 1992-1993, 1994-1995, and 1997-1998 seasons; 3) dramatic fluctuations in feral pig populations (e.g., crash in 1990 and 1991); 4) dramatic increases in coverage by introduced weeds, especially fennel since 1992 due to release from grazing animals and enhanced by rains after drought; and 5) introduction (1988) and spread of the exotic, cavity-nesting, leafcutting bee, *Megachile apicalis*.

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