Appendix 2. Herbaceous vascular plant species recorded from plots monitoring the recovery of vegetation from feral sheep grazing. Santa Cruz Island, California, 1984–1993.

Species	Relative frequency
Native annual grasses	
Bromus carinatus	0.003
Bromus maritimus	0.030
Hordeum californicum	0.050
Hordeum depressum	0.402
Native annual herbs	
Achyrachaena mollis	0.027
Agoseris heterophylla	0.055
Amsinckia intermedia	0.096
Amsinckia menziesii	0.045
Antirrhinum nuttallianum	0.002
Astragalus didymocarpus	0.151
Bowlesia incana	0.040
Calandrinia ciliata	0.264
Camissonia robusta	0.007
Charizanthe staticoides	0.040
Claytonia perfoliata	0.101
Crassula erecta	2.004
Cryptantha clevelandii	0.030
Daucus pusillus	0.148
Dodecatheon clevlandi	0.007
Eremocarpus setigerus	4.423
Erodium macrophyllum	0.089
Eschscholzia californica	0.002
Filago arizonica	0.805
Filago californica	1.125
Gilia angelensis	0.289
Gilia clivorum	0.034
Gnaphalium bicolor	0.119
Gnaphalium californicum	0.015
Gnaphalium chilense	0.055
Gnaphalium microcephalum	0.709
Hemizonia fasciculata	0.099
Heterotheca grandiflora	1.592
Lasthenia californica	0.941
Layia platyglossa	0.214
Lepidium nitidum	1.069
Linanthus androsaceus	0.002
Linaria texana	0.002
Lotus micranthus	0.078
Lotus strigosus	0.081
Lotus subpinnatus	0.414
Lupinus bicolor	0.989
Micropus californicus	2.345
Montia fontana	0.005
Navarretia atractyloides	0.124
Orthocarpus attenuatus	0.163
Orthocarpus purpurascens	0.010
Pectocarya linearis	0.114
Plagiobothrys canescens	0.003
Plagiobothrys collinus	0.124
Psilocarphus tenellus	0.177
Pterostygia drymarioides	0.020
Ranunculus californicus	0.044
Spergularia marina	0.131
Stylocline gnaphalioides	0.479
Thysanocarpus curvipes	0.008
Trifolium albopurpureum	0.479
Trifolium amplectens	1.835
Trifolium ciliolatum	0.002
Trifolium depauteratum	0.002
Trifolium fucatum	0.044
Trifolium gracilentum	0.045
Trifolium microcephalum	1.056
Trifolium microdon	0.437
Trifolium tridentatum	0.010
Trifolium variegatum	0.012
Viola pedunculata	0.795
Native perennial grasses	
Aristida adscensionis	0.108
Aristida divericata	0.434
Stipa cernua	0.015
Stipa diegoensis	0.143
Stipa lepida	0.126
Stipa pulchra	2.668
Native perennial herbs	
Achillea millefolium	0.010
Native perennial herbs (continued)	
Allium praecox	0.025
Asclepias fascicularis	0.008
Atriplex californica	0.134
Bloomeria crocea	0.214
Brodiaea jolonensis	0.018
Calochortus albus	0.003
Calystegia macrostegia	0.077
Cardionema ramosissimum	0.546
Chenopodium californicum	0.045
Cirsium occidentale	0.003
Dichelostemma pulchellum	0.662
Epilobium ciliatum	0.005
Frankenia salina	0.042
Galium angustifolium	0.003
Galium nuttallii	0.007
Lomatium utriculatum	0.002
Lupinus concinnus	0.077
Marah macrocarpus	0.010
Sanicula arguta	0.099
Scutellaria tuberosa	0.017
Sidalcea malviflora	0.044
Sisyrinchium bellum	0.082
Stachys bullata	0.008
Zauschneria californica	0.024
Nonnative perennial grasses	
Avena barbata	10.652
Avena fatua	0.229
Bromus diandrus	4.724
Bromus mollis	8.954
Bromus rubens	6.131
Gastridium ventricosum	0.109
Hordeum geniculatum	0.338
Hordeum leporinum	1.128
Hordeum murinum	0.091
Lamarkia aurea	1.503
Lolium multiflorum	0.079
Lolium perenne	0.054
Parapholis incurva	0.018
Phalaris minor	0.392
Vulpia bromoides	0.953
Vulpia myuros	4.788
Nonnative annual herbs	
Anagallis arvensis	0.212
Brassica geniculata	0.008
Brassica nigra	0.639
Capsella bursa-pastoris	0.008
Centaurea melitensis	1.261
Centaurea solstitialis	0.136
Cerastium glomeratum	0.435
Erodium botrys	3.401
Erodium cicutarium	6.219
Erodium moschatum	0.274
Galium aparine	0.136
Gnaphalium luteo-album	0.059
Hypochoeris glabra	5.314
Madia sativa	0.008
Malva parviflora	0.092
Matricaria matricarioides	0.002
Medicago polymorpha	3.300
Rigiopappus leptocladus	0.062
Senecio vulgaris	0.131
Silene gallica	4.494
Silybum marianum	0.039
Sisymbrium officinale	0.030
Sonchus asper	0.249
Sonchus oleraceous	0.313
Spergula arvensis	0.003
Stellaria media	0.301
Torilis nodosa	0.205
Nonnative perennial herbs	
Aster chilensis	0.002
Atriplex semibaccata	0.893
Convolvulus arvensis	0.397
Cotula australis	0.050
Foeniculum vulgare	0.343
Rumex crispus	0.061

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Flowers Visited by Honey Bees and Native Bees on Santa Cruz Island

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Abstract. European honey bees (*Apis mellifera* L.) were introduced to Santa Cruz Island more than 110 yr ago. Feral honey bee populations occupy most of the island and share floral resources with many native bees. Studies are being conducted to determine the impact of honey bees on native bees and pollination of flowering plants on Santa Cruz Island, as well as the effects of removal of honey bees from a closed system. Foraging honey bees tend to concentrate on introduced weedy plant species. Honey bees overlap primarily with generalist native bees in exploitation of pollen and nectar resources. Removal of honey bees from Santa Cruz Island is predicted to (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.

Keywords: Feral honey bees; *Apis mellifera*; Africanized honey bees; native bees; nonnative bees; nonnative weeds; endemic plants; biodiversity; biogeography; food resource use; food resource overlap; pollen; nectar; pollination; keystone species; Santa Cruz Island.

Introduction

Considerable controversy exists regarding the impact of honey bees, (*Apis mellifera* L.), on the flora and fauna of various areas of the world where it has been introduced by humans (Roubik 1989; Pyke 1990; Wills et al. 1990; Sugden and Pyke 1991; and Paton 1993). Most were races of European honey bees (EHB) introduced to provide honey and beeswax. More recently a genotype from Africa introduced to Brazil to improve honey production has spread rapidly through the Americas displacing European strains in tropical and subtropical areas. This is the African or Africanized honey bee (AHB) that has received so much attention in the popular press (often known as "killer bees") due to their vigorous colony defense behavior that has resulted in numerous domestic animal and human deaths in the areas they have invaded. This genetic type has become established in Texas (since 1990), Arizona (since 1992) and most recently in New Mexico (1993), and is expected to arrive in California any time.

In most areas of introduction, honey bees have successfully established feral populations by swarming from commercial colonies and have become naturalized. Feral colonies differ from commercial colonies in many characteristics: smaller colony populations, smaller nest cavity size, continued presence if environment permits, and frequent swarming (Seeley 1985; Thorp 1987). These features affect the potential impact on local flora and competition with native bees. Densities of commercial honey bee colonies can be controlled and their effects may be intense, but temporary and sporadic. Densities of feral EHB colonies and their population sizes are greatly affected by fluctuations in floral and water resources. Densities of feral AHB are reported to be greater than those of EHB in tropical areas due to smaller colony sizes, nest cavities occupied, and more frequent swarming (Roubik 1989).

Honey bees were introduced to Santa Cruz Island before 1880 (Wenner and Thorp 1993, 1994). Wenner (1989) proposed a phased removal of them from Santa Cruz Island along with studies on concomitant changes in the flora and fauna. Because honey bees have not become established on any of the other northern Channel Islands, this appears to be a unique opportunity to evaluate the impact of removal of honey bees from a closed system, an opportunity not feasible in mainland habitats due to the widespread naturalization of feral populations. Thus, we set out to determine the diversity of plants used as pollen and/or nectar resources by honey bees in comparison to those used by native bees on Santa Cruz Island. This was deemed basic to questions as to the extent of resource sharing and where to look for the most intensive overlap and, thus, potential competition for food. In order to compare interactions for floral resources between honey bees and other bees on Santa Cruz Island with those of mainland communities, we also investigated the biodiversity, floral specializations, and biogeographic origins of the native bee fauna on Santa Cruz Island.

These studies have been conducted against a background of many dynamic changes on Santa Cruz Island. We started our studies in 1988 near the beginning of a 6-yr drought cycle; cattle and sheep removal was just being completed and feral pig populations were high. During the drought, pig populations crashed in the summer/fall of 1989 and 1990. Aseasonal rains in March 1991 and February 1992 and the above normal rainfall of 1992–93 coincided with explosive increases of fennel, mustard, horehound, and yellow star-thistle, and the appearance of some native plants and bees that had not been seen on Santa Cruz Island in many years (S. Junak and R. W. Thorp, pers. obs.).

Table 1. Additions to the list of bees species found on Santa Cruz Island by Rust et al. (1985).

Andrenidae
Andrena (*Derandrena*) *vandykei* Cockerell[1]
Andrena (*Diandrena*) *submoesta* Viereck[2]
Andrena (*Erandrena*) *principalis* LaBerge
Andrena (*Euandrena*) *chlorura* Cockerell[2]
Andrena (*Hesperandrena*) sp. 1
Andrena (*Hesperandrena*) sp. 2
Andrena (*Onagrandrena*) *oenotherae* Timberlake[3]
Andrena (*Simandrena*) *angustitarsata* Viereck[4]
Andrena (*Simandrena*) *pallidifovea* (Viereck)[1]
Andrena (*Tylandrena*) *subaustralis* Cockerell[2]
Andrena (*Tylandrena*) *subtilis* Smith[1]

Halictidae
Halictus ligatus Say

Megachilidae
Protosmia (=*Chelostomopsis*) *rubifloris* (Cockerell)[2]
Osmia (*Cephalosmia*) *californica* Cresson[3]
Osmia (*Chalcosmia*) *coloradensis* Cresson
Osmia (*Chenosmia*) nr. *exigua* Cresson
Megachile (*Eutricharaea*) *apicalis* Spinola
Megachile (*Sayapis*) sp.

Anthophoridae
Exomalopsis cerei Timberlake
Anthophora californica Cresson[2]
Habropoda depressa Fowler[2]
Habropoda miserabilis (Cresson)[2]
Melecta separata callura (Cockerell)[2]
Xeromelecta californica (Cresson)[2]

Apidae
Bombus (*Crotchiibombus*) *crotchii* Cresson[2]
Bombus (*Fervidobombus*) *californicus* Smith[2]
Bombus (*Pyrobombus*) *edwardsii* Cresson[3]
Bombus (*Pyrobombus*) *vosnesenskii* Radoszkowski[2]

[1] Listed as *Andrena* sp. by Rust et al. (1985).
[2] Recorded from other Channel Islands (Rust et al. 1985).
[3] Listed as unconfirmed literature record by Rust et al. (1985).
[4] Listed as *Andrena* (*Simandrena*) sp. by Rust et al. (1985).

Biodiversity and Floral Specialization

The bee fauna on Santa Cruz Island has the greatest species diversity found on any of the Channel Islands (Rust et al. 1985). This is directly related to the size, maximum elevation, index of topographic diversity, numbers of plant species and communities, and proximity to the mainland of Santa Cruz Island (Rust et al. 1985). During the past 5 yr, we have increased the number of catalogued bee species on Santa Cruz Island by 25% (Table 1). Similar additions were made to the faunal list of Santa Rosa Island on the basis of a 1 weekend trip by one of us (R. W. Thorp) during which 20 species of bees were collected with 7 (18%) being new to the list of 39 species by Rust et al. (1985). Since these additions indicate that the Channel Islands bee faunas are considerably underestimated, we will not attempt at this time to reassess the inter-island biogeographic analyses of Rust et al. (1985) without further effort to collect on other Channel Islands. Rather, we will focus below on the relationship of the bee fauna of Santa Cruz Island to broader scale biogeographic patterns and analyze the detailed information we have developed on their floral resource use.

Few studies have analyzed local or regional bee faunas in California (Moldenke 1976; Rust et al. 1985; Thorp and Gordon 1992; Dobson 1993). The bee fauna of Santa Cruz Island seems most comparable to the coastal dunes and sage region of Moldenke (1976) in numbers of bee species (diversity) and percentage of specialists. However, the island is more than a coastal community type. The presence of a central valley bounded by south and north ranges attaining greater than 750 m elevation, makes it more comparable to mainland areas of the south coast ranges, including the coast. Moldenke (1976) estimates that there are about 520 species of bees in the southern California Coast Ranges (Table 2) and that slightly more than 50% of these are specialists (oligoleges) limited to 1 or a few closely related host plants as pollen resources (Robertson 1925; Linsley and MacSwain 1958). The total number of bee species we have recorded on Santa Cruz Island to date is 105 with less than 20% being specialists. All of the Colletidae, Halictidae, and Apidae are generalists. Of the other bee families 44% of the Andrenidae, 21.7% of the Megachilidae, and 11.8% of the Anthophoridae are specialists.

Phenology of bee activity at flowers on Santa Cruz Island approximate the patterns documented by Robertson (1925, 1929) with specialists having short activity periods in comparison with generalists. Most of the oligoleges on Santa Cruz Island, especially species of *Andrena* and *Synhalonia*, fly for 1–3 mo during the early part of the year, January through May or occasionally into early June. While generalists (polyleges) fly much of the year. Our biodiversity records on Santa Cruz Island cover January through October and we find *Apis* and *Dialictus* at flowers during the entire period. *Colletes*, *Augochlorella*, *Evylaeus*, and *Anthidium* are at flowers from March through October and *Anthidium*, *Ceratina*, *Agapostemon*, *Melissodes*, *Hylaeus*, and *Megachile* are on the wing for 6–7 mo.

Table 2. Diversity of bee species by family on Santa Cruz Island, all Channel Islands, and southern California Coast Ranges.

	Present		Rust et al. (1985)				Moldenke (1976)	
	Santa Cruz Island		Santa Cruz Island		All Channel Islands		S. Cal. Coast Ranges	
Family	No.	(%)	No.	(%)	No.	(%)	No.	(%)
Colletidae	2	(1.9)	2	(2.4)	2	(1.3)	21	(4.0)
Andrenidae	25	(23.8)	19	(22.5)	31	(20.3)	136	(26.2)
Halictidae	16	(15.2)	15	(17.9)	38	(24.8)	89	(17.1)
Melittidae	0	(0.0)	0	(0.0)	0	(0.0)	2	(0.4)
Megachilidae	23	(21.9)	18	(21.4)	26	(17.0)	132	(25.4)
Anthophoridae	34	(32.4)	28	(33.3)	49	(32.0)	132	(25.4)
Apidae	5	(4.8)	2	(2.4)	7	(4.6)	8	(1.5)
Totals	105		84		153		520	

Biogeography

We find that Santa Cruz Island has a depauperate bee fauna as is typical of many island faunas (MacArthur and Wilson 1967; Carlquist 1974). Species:genus ratios are 3.1 on Santa Cruz Island vs 11.6 for California, and species: family ratios are 17.5 for Santa Cruz Island vs 74.3 for southern California Coast Ranges. Representations of bee families on Santa Cruz Island are similar to those presented in Rust et al. (1985) and Moldenke (1976) for southern California Coast Ranges with the exceptions that no Melittidae have been found (Table 2). The percentage of Anthophoridae is higher on Santa Cruz Island and the other Channel Islands than on the mainland, while the percentage of Halictidae is higher on all other Channel Islands than on Santa Cruz Island and the mainland (Table 2).

Most of the bee species on Santa Cruz Island have their distributions confined to the western United States (Table 3). The next highest representations are from the Pacific Coast (27.5%) or restricted to California (24%). These patterns of distribution are similar to those found by Thorp and Gordon (1992) for bees at Bodega Bay, California. However, on Santa Cruz Island, there are no native bee species with Holarctic distributions and only 2 taxa, *Perdita layiae layiae* (Cockerell) and *Lasioglossum channelense* McGinley (Rust in Miller 1985, McGinley 1986), that are considered endemic to the northern Channel Islands.

Table 3. Biogeographic relationships of bee species found on Santa Cruz Island, California.

Biogeography	No.	(%)
Holarctic (H)	0	(0.0)
Transcontinental (T)	3	(3.5)
W No America (W US)	37	(42.5)
Pacific Coast (PC)	24	(27.5)
California (CA)	13	(15.0)
So California (So CA)	7	(8.0)
Island Endemic (EE)	1	(1.0)
Introduced (**)	2	(2.5)
Total	87	(100.0)

Flowers Visited by Honey Bees

Honey bees on Santa Cruz Island have been found visiting flowers of 57 species of plants, out of 154 flowering plants studied (Table 4, Appendices 1 and 3). They exhibit a strong tendency to use introduced flowering plants as their primary sources of pollen and nectar (Table 4). Since our studies began in 1988, we have observed that more than 35% of the flower species visited by *Apis* are introduced species. Nonnative plant species constitute some of the most preferred resources for honey bees based on their relative abundance visiting such flowers as eucalyptus (*Eucalyptus* spp.), mustard (*Brassica* spp.), horehound (*Marrubium vulgare*), and yellow star-thistle

Table 4. Flowering plant species and bee visitation on Santa Cruz Island.

	Visited by *Apis*			Not visited by *Apis*[1]		
Plant type	*Apis* only	*Apis* and other bees	Total	Visited by other bees	No visits[2] by bees	Total visited by non-*Apis*
Endemic	0	7	7	1	2	8
Native	4	26	30	41	29	67
Introduced	3	17	20	12	12	29
Totals	7	50	57	54	43	104

[1] Some of these plants are known to be visited by honey bees in other localities, but conditions at the time of observation (e.g., distance from nearest feral colony, weather, flower population size, time of season, time of day) and limited numbers of observations require further investigation. We expect that these numbers will be modified after further study.

[2] Lack of observed visits during this study may be due to small sample sizes, or observations taken at times when bees are not active. We expect that these numbers will be modified with further study.

(*Centaurea solstitialis*). Many of the native flowering plant species visited by *Apis* have a generalized bee/wasp pollination syndrome. Honey bees have been observed foraging on Santa Cruz Island endemics including: Santa Cruz Island ironwood (*Lyonothamnus floribundus asplenifolius*), cliff-aster (*Malacothrix saxatilis implicata*), and Santa Cruz Island live-forever (*Dudleya nesiotica*). However, in all instances, honey bees were rare visitors and did not appear to have a significant impact on the reproduction of these plants, nor did they appear to compete significantly with native pollinators of these plants.

Roubik (1989) found that at the level of the flower patch, AHB displaced native bees, but that in other experiments he was unable to show any negative impact of Africanized honey bees on colony food storage or brood production of stingless bees. Our measures of bee diversity and abundance at flowers demonstrate a similar inverse relationship between abundance of honey bees and native bees on populations of *Arctostaphylos* in 1992 and over several years along a transect consisting mainly of *Foeniculum* and *Centaurea* (Wenner and Thorp 1994). We will be able to better test the impact of honey bees on native bees in the future, since we have located nest sites of several bee species and are monitoring cavity nesting bees using trap-nests as in mainland studies by Thorp et al. (1992).

Flowers and Bee Guilds

Of the 57 species of flowering plants visited by honey bees, 50 are shared with native bees (Table 4 and Appendix 2). Most of this overlap is with native bees that are generalists in their pollen host preferences, rather than those that specialize on one or a few closely related species as their sole sources of pollen (oligoleges). The guilds of bee species sharing resources of a flower species with honey bees range in species diversity from 1 native species each on *Baccharis pilularis* and *Toxicodendron diversilobus*, to about 25 species (Appendix 2). Flowering plants with the largest bee guilds include *Brassica* (25+), *Centaurea solstitialis* (25), *Grindelia* (22), *Cakile* (21), *Marrubium* (17), *Malacothrix* (16), and *Silybum* (16). Of these, only *Grindelia* and *Malacothrix* are native or endemic to Santa Cruz Island.

A nonnative plant species of concern, *Centaurea solstitialis*, and native plant, *Grindelia robusta*, that we have emphasized in our studies show considerable overlap in the guilds of bees that visit them, but the relative abundance of visitors to each is quite different (Table 5). The recently introduced leafcutting bee, *Megachile apicalis*, makes use of both plants on Santa Cruz Island. It has developed a widespread association with both plants on the mainland also, especially throughout the Central Valley of California.

Discussion and Conclusions

Honey bees are generalist (polylectic) foragers. Wills et al. (1990) found that they visited only 30% of 413 flowering plant species and that they preferentially foraged on the most common species available. Donovan (1980) found that honey bees exhibited a strong tendency to forage on introduced weedy flora in New Zealand. Our findings on Santa Cruz Island are similar to both of these studies (Table 4, Appendices 1 and 3).

Overall, the proportion of plants visited by honey bees that are introduced species (35%), is higher than the proportion visited by native bee species (28%) (Table 4). The difference between these proportions is even more impressive when one considers the difference in scale of taxonomic diversity among the 2 categories of bees.

Table 5. Species diversity and relative abundance of bee visitor guilds at flowering heads of the introduced *Centaurea solstitialis* (yellow star-thistle) and the native *Grindelia robusta* (gum plant) on Santa Cruz Island (1988–1993).

	Relative abundance[1] on:	
Bee taxa	*Centaurea*	*Grindelia*
Agapostemon texanus	+++	++
Anthidium maculosum	+	+
Anthophora urbana	+	0
Apis mellifera	++++	++
Ashmeadiella sp.	+	++
Augochlorella pomoniella	+++	++++
Bombus edwardsii	+	0
Ceratina acantha	+++	++
Diadasia rinconis	++	+
Dialictus sp.	+	+
Epeolus sp. 1	+	++
Epeolus sp. 2	0	+
Evylaeus sp. 1	+	0
Evylaeus sp. 2	+	0
Exomalopsis cerei	+	0
Halictus ligatus	+	+
Halictus (*Seladonia*) sp.	+	+
Hylaeus sp.	+	+
Megachile apicalis	++	+
Megachile sp. 1	+++	++
Megachile sp. 2	+	+
Megachile sp. 3	0	+
Megachile (*Sayapis*) sp.	+	+
Melissodes sp.	+++	++++
Nomada sp.	+	+
Osmia sp.	+	+
Triepeolus sp.	+	++

[1] Number of bee species observed:
+ ≤ 15 ++ = 15–49 observations
+++ = 50–100 observations ++++ ≥ 100 observations
0 = bee species not observed on this plant

While the introduced honey bee is a single species, the native bees comprise 105 species and 34 genera in 6 families. This difference makes a statistical comparison inappropriate. Interesting comparisons between honey bees and individual native bee species may still be feasible when our database of diversity and flower relationships is more complete.

Removal of honey bees from Santa Cruz Island presents us with an unique opportunity to test questions about the impact of honey bees in a large closed system. The hypotheses relating to honey bee removal we plan to test include (1) many generalist native bees will exhibit competitive release; (2) most specialist (oligolectic) native bees will not exhibit competitive release; (3) reproductive success of some introduced weedy flowering plants will be reduced; and (4) reproductive success of many native flowering plants will be increased due to anticipated increases in native bee populations.

Another important question that can be tested by removing EHB from Santa Cruz Island is whether or not AHB can invade across a water barrier of 30 km. Since EHB have not crossed the 9 km between Santa Cruz Island and Santa Rosa Island, this seems unlikely. However, Roubik (1989) states that AHB have crossed 32 km of water to uninhabited islands and that greater distances are possible. Thus, monitoring for subsequent invasions of the island by Africanized honey bees will be needed. If AHB can invade and establish, the techniques for efficient location of feral honey bee colonies developed by Wenner et al. (1992) will be crucial in keeping Santa Cruz Island free of AHB.

Thorp and Gordon (1992) considered bees "keystone" species because of their importance to plant communities in the process of pollination. Mills et al. (1993) argue that the keystone-species concept has been extended greatly beyond its original definition and that it is largely undemonstrated, places undue emphasis on duality of species rankings, lacks focus on interactions, and, therefore, is potentially harmful if formalized in laws with rigid practical conservation implications. Kevin (1990) applied the term keystone to the process of pollination. Regardless of terminology, species interactions between bees through resource overlap, and between bees and plants through pollination are the critical processes on which our studies focus.

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Appendix 1. Cumulative list of flowers visited by honey bees on Santa Cruz Island 1988–1993.

Flowers	Status[1]	Preferred by *Apis*[2] for[3]		Visited by Non-*Apis* bees[4]
Acacia melanoxylon (blackwood acacia)	I	(P)	+	–
Adenostema fasciculatum (chamise)	N	(PN)	+	+
Arctostaphylos sp. (manzanita)	E	N	++	+
Asclepias fascicularis (milkweed)	N	N	+++	+
Astragalus miguelensis (locoweed)	N	(N)	+	+
Baccharis douglasii (Douglas' baccharis)	N	(PN)	++	+
Baccharis glutinosa (mulefat)	N	PN	+++	+
Baccharis pilularis (coyote brush)	N	PN	++	+
Brassica sp. (mustard)	I	PN	++++	+
Cakile maritima (sea rocket)	I	PN	++	+
Calystegia macrostegia (island morning glory)	E	(N)	+	+
Cardaria draba (hoary cress)	I	(N)	+	+
Ceanothus arboreus (island ceanothus)	E	PN	+	+
Ceanothus megacarpus (island bigpod ceanothus)	N	PN	+	+
Centaurea melitensis (tocalote)	I	PN	+	+
Centaurea solstitialis (yellow star-thistle)	I	PN	++++	+
Cichorium intybus (chicory)	I	PN	+	+
Citrus spp. (orange and grapefruit)	I	N	++++	+
Clematis ligusticifolia (creek clematis)	N	(N)	++	–
Cynara scolymus (artichoke)	I	(N)	+	+
Datura innoxia (Jimson weed)	N	PN	+	+
Dudleya nesiotica (Santa Cruz Island live-forever)	EEL	(N)	+	+
Eremocarpus setigerus (dove weed)	N	N	++	+
Eriogonum arborescens (Santa Cruz Island buckwheat)	E	PN	+	+
Eriogonum grande (island buckwheat)	N	PN	+	+
Erodium sp. (filaree)	I	PN	+++	+
Eschscholzia californica (California poppy)	N	P	+	+
Eucalyptus camaldulensis (red gum)	I	PN	++++	+
Eucalyptus globulus (blue gum)	I	N	++++	–
Foeniculum vulgare (sweet fennel)	I	PN	+++	+
Grindelia robusta (gum plant)	N	PN	+	+
Heteromeles arbutifolia (toyon)	N	PN	+++	+

Appendix 1 (continued).

Flowers	Status[1]	Preferred by *Apis*[2] for[3]		Visited by Non-*Apis* bees[4]
Heterotheca grandiflora (telegraph weed)	N	PN	+	+
Keckiella cordifolia (climbing penstemon)	N	N	+	+
Lepidospartum squamatum (scale broom)	N	(PN)	+	–
Lotus corniculatus (bird's foot trefoil)	I	PN	+++	+
Lotus grandiflorus (chaparral lotus)	N	(N)	+	+
Lotus scoparius (deerweed)	N	(N)	+	+
Lyonothamnus floribundus (Santa Cruz Island ironwood)	EL	PN	+	+
Malacothrix saxatilis (cliff aster)	E	(N)	+	+
Malus sylvestris (apple)	I	(N)	+	+
Marrubium vulgare (horehound)	I	N	++++	+
Mimulus longiflorus (bush monkeyflower)	N	PN	+	+
Mirabalis californica (wishbone bush)	N	(N)	+	–
Phacelia distans (wild heliotrope)	N	PN	+	+
Phacelia viscida (sticky phacelia)	N	PN	+	–
Pholistoma auritum (fiesta flower)	N	(PN)	+	+
Plantago lanceolata (narrow-leaved plantain)	I	P	+	+
Prunus ilicifolia lyonii (island cherry)	N	(PN)	++++	+
Quercus sp. (oak)	N	P	+	+
Rhus integrifolia (lemonadeberry)	N	PN	++	+
Robinia pseudo-acacia (black locust)	I	N	+++	+
Salvia mellifera (black sage)	N	N	++++	+
Schinus molle (Peruvian pepper tree)	I	(PN)	++	–
Senecio douglasii (bush groundsel)	N	PN	++	+
Silybum marianum (milk thistle)	I	(N)	+++	+
Toxicodendron diversilobum (poison oak)	N	PN	++++	+

[1] **E** = endemic; **EE** = Santa Cruz Island only; **L** = listed; **N** = native; **I** = introduced.
[2] + = lowest preference; ++++ = highest preference.
[3] **P** = pollen; **N** = nectar; **PN** = both pollen and nectar; () = insufficient data.
[4] + = other bees visit; – = no other bees have been found visiting.

Appendix 2. Food resource sharing: flowers visited by *Apis* and the guilds of other bees that visit them on Santa Cruz Island, California, 1988–1993.

Adenostema fasciculatum (chamise)

Agapostemon texanus, Augochlorella pomoniella, Dialictus sp., *Evylaeus* sp., *Megachile* sp., *Osmia* sp.

Arctostaphylos sp. (manzanita)

Andrena principalis, Andrena vandykei, Bombus edwardsii, Dialictus sp., *Evylaeus* sp., *Habropoda depressa, Nomada* spp.

Asclepias fascicularis (milkweed)

Dialictus sp., *Megachile* spp.

Astragalus miguelensis (locoweed)

Andrena oenotherae, Anthophora californica, Anthophora edwardsii, Bombus californicus, Bombus crotchii, Bombus vosnesenskii, Osmia sp., *Synhalonia* sp.

Baccharis douglasii (Douglas' baccharis)

Colletes sp.

Baccharis glutinosa (mulefat)

Agapostemon texanus, Anthidium maculosum, Augochlorella pomoniella, Bombus edwardsii, Colletes sp., *Dialictus* spp., *Hylaeus* sp., *Nomada* spp.

Baccharis pilularis (coyote brush)

Augochlorella pomoniella, Colletes sp.

Brassica sp. (mustard)

Agapostemon texanus, Andrena prunorum, Andrena sp., *Anthidium maculosum, Anthophora urbana, Augochlorella pomoniella, Bombus edwardsii, Ceratina acantha, Colletes* sp., *Dialictus* spp., *Epeolus* sp., *Evylaeus* sp., *Halictus* (*Seladonia*) sp., *Hylaeus* sp., *Lasioglossum* spp., *Megachile* spp., *Melissodes* sp., *Nomada* sp., *Osmia* spp., *Synhalonia* sp., *Triepeolus* sp.

Cakile maritima (sea rocket)

Agapostemon texanus, Andrena oenotherae, Andrena prunorum, Andrena sp., *Anthidium maculosum, Anthophora californica, Anthophora edwardsii, Anthophora urbana, Ashmeadiella* sp., *Augochlorella pomoniella, Bombus edwardsii, Ceratina acantha, Colletes* sp., *Dialictus* sp., *Evylaeus* sp., *Habropoda miserabilis, Lasioglossum* sp., *Megachile* spp., *Megachile* (*Sayapis*) sp., *Melecta separata callura, Osmia* sp.

Calystegia macrostegia (island morning glory)

Agapostemon texanus, Augochlorella pomoniella, Colletes sp., *Diadasia bituberculata, Diadasia rinconis, Dialictus* sp., *Evylaeus* sp., *Habropoda depressa, Nomada* sp., *Osmia* sp., *Synhalonia* sp.

Cardaria draba (hoary cress)

Nomada sp.

Ceanothus arboreus (island ceanothus)

Andrena sp., *Dialictus* sp., *Habropoda depressa, Hylaeus* sp., *Panurginus* sp.

Appendix 2 (continued).

Ceanothus megacarpus (island bigpod ceanothus)

Andrena candida, Andrena chlorura, Dialictus sp., *Panurginus* sp.

Centaurea melitensis (tocalote)

Agapostemon texanus, Anthidium sp., *Augochlorella pomoniella, Ceratina* sp., *Dialictus* sp., *Halictus* (*Seladonia*) sp., *Megachile apicalis, Melissodes* sp., *Nomada* sp.

Centaurea solstitialis (yellow star-thistle) (See Table 5)

Cichorium intybus (chicory)

Agapostemon texanus, Andrena prunorum, Augochlorella pomoniella, Ceratina sp., *Colletes* sp., *Dialictus* sp., *Evylaeus* sp., *Lasioglossum* sp., *Melissodes* sp., *Sphecodes* sp.

Citrus spp. (orange and grapefruit)

Augochlorella pomoniella, Dialictus sp., *Evylaeus* sp.

Cynara scolymus (artichoke)

Agapostemon texanus, Augochlorella pomoniella, Diadasia rinconis.

Datura innoxia (Jimson weed)

Agapostemon texanus, Anthophora urbana, Augochlorella pomoniella, Ceratina sp., *Diadasia rinconis, Dialictus* sp., *Evylaeus* sp., *Halictus tripartitus, Lasioglossum* sp.

Dudleya nesiotica (Santa Cruz Island live-forever)

Agapostemon texanus, Anthidium sp., *Colletes* sp., *Dialictus* sp., *Melissodes* sp.

Eremocarpus setigerus (dove weed)

Dialictus sp., *Halictus* (*Seladonia*) sp.

Eriogonum arborescens (Santa Cruz Island buckwheat)

Agapostemon texanus, Andrena sp., *Anthidium* sp., *Anthophora californica, Augochlorella pomoniella, Ceratina* sp., *Colletes* sp., *Dialictus* sp., *Hylaeus polifolii, Megachile* sp.

Eriogonum grande (island buckwheat)

Agapostemon texanus, Augochlorella pomoniella, Ceratina sp., *Colletes* sp., *Dialictus* sp., *Epeolus* sp., *Evylaeus* sp., *Hylaeus* sp., *Megachile* sp., *Melissodes* sp., *Nomada* sp., *Triepeolus* sp.

Erodium sp. (filaree)

Halictidae sp.

Eschscholzia californica (California poppy)

Augochlorella pomoniella, Ceratina sp., *Evylaeus* sp., *Megachile* spp.

Eucalyptus camaldulensis (red gum)

Andrena sp., *Colletes* sp., *Dialictus* sp., *Halictus* (*Seladonia*) sp., *Hylaeus* sp., *Lasioglossum* sp., *Megachile* sp.

Foeniculum vulgare (sweet fennel)

Agapostemon texanus, Augochlorella pomoniella, Evylaeus sp., *Lasioglossum* sp., *Megachile* sp.

Grindelia robusta (gum plant) (See Table 5)

Appendix 2 (continued).

Heteromeles arbutifolia (toyon)

Agapostemon texanus, Ashmeadiella sp., *Augochlorella pomoniella, Bombus edwardsii, Ceratina* sp., *Colletes* sp., *Dialictus* sp., *Evylaeus* sp., *Halictus* (*Seladonia*) sp., *Hylaeus* sp., *Megachile* sp.

Heterotheca grandiflora (telegraph weed)

Ceratina sp., *Dialictus* sp., *Melissodes* sp.

Keckiella cordifolia (climbing penstemon)

Augochlorella pomoniella, Bombus edwardsii, Ceratina sp., *Dialictus* sp., *Evylaeus* sp., *Lasioglossum* sp., *Megachile* sp.

Lotus corniculatus (bird's foot trefoil)

Anthidium spp., *Anthophora urbana, Bombus californicus, Bombus crotchii, Megachile* spp., *Megachile* (*Sayapis*) sp., *Xeromelecta californica.*

Lotus grandiflorus (chaparral lotus)

Anthidium sp., *Augochlorella pomoniella, Bombus edwardsii, Habropoda depressa,* Megachilidae sp., *Melissodes* sp., *Osmia* sp., *Synhalonia* sp.

Lotus scoparius (deerweed)

Anthidium maculosum, Bombus edwardsii, Colletes sp., *Habropoda depressa, Lasioglossum* sp., *Megachile* sp., *Osmia* sp., *Synhalonia* sp.

Lyonothamnus floribundus (Santa Cruz Island ironwood)

Dialictus sp., *Evylaeus* spp., *Lasioglossum* sp.

Malacothrix saxatilis (cliff aster)

Agapostemon texanus, Anthidium sp., *Ashmeadiella* sp., *Augochlorella pomoniella, Bombus californicus, Bombus edwardsii, Ceratina acantha, Colletes* sp., *Diadasia rinconis, Dialictus* sp., *Evylaeus* sp., *Halictus* (*Seladonia*) sp., *Megachile* sp., *Melissodes* sp., *Nomada* sp., *Osmia* sp.

Marrubium vulgare (horehound)

Agapostemon texanus, Anthidium maculosum, Anthophora urbana, Augochlorella pomoniella, Bombus edwardsii, Ceratina acantha, Diadasia rinconis, Dialictus sp., *Epeolus* sp., *Evylaeus* sp., *Megachile* spp., *Melissodes* sp., *Nomada* sp., *Osmia* sp., *Triepeolus* sp., *Xeromelecta californica.*

Mimulus longiflorus (bush monkeyflower)

Anthophora californica, Augochlorella pomoniella, Ceratina acantha, Diadasia rinconis, Osmia spp., *Synhalonia* sp.

Phacelia distans (wild heliotrope)

Andrena sp., *Anthidium* sp., *Anthophora californica, Bombus edwardsii, Ceratina acantha, Dialictus* sp., *Evylaeus* sp., *Habropoda depressa.*

Pholistoma auritum (fiesta flower)

Anthophora sp., *Habropoda* sp.

Plantago lanceolata (narrow-leaved plantain)

Anthophora urbana, Augochlorella pomoniella, Colletes sp., *Dialictus* sp., *Evylaeus* sp., *Habropoda depressa, Synhalonia* sp.

Appendix 2 (continued).

Prunus ilicifolia lyonii (island cherry)

Andrena sp., *Colletes* sp., *Hylaeus* sp.

Quercus sp. (oak)

Bombus edwardsii.

Rhus integrifolia (lemonadeberry)

Augochlorella pomoniella, Halictidae sp.

Robinia pseudo-acacia (black locust)

Bombus edwardsii.

Salvia mellifera (black sage)

Anthidium maculosum, Anthophora californica, Bombus edwardsii, Habropoda depressa.

Senecio douglasii (bush groundsel)

Agapostemon texanus, Ceratina sp., *Epeolus* sp., *Hylaeus* sp., *Megachile* sp., *Triepeolus* sp.

Silybum marianum (milk thistle)

Agapostemon texanus, Anthophora urbana, Augochlorella pomoniella, Bombus californicus, Bombus edwardsii, Ceratina acantha, Diadasia rinconis, Dialictus sp., *Evylaeus* spp., *Halictus ligatus, Lasioglossum* sp., *Megachile apicalis, Melissodes* sp., *Osmia* sp., *Synhalonia* sp.

Toxicodendron diversilobum (poison oak)

Andrena sp.

Appendix 3. Monitored flowers of Santa Cruz Island that were not visited by honey bees, 1988–1993.

Flowers	Status[1]	Visited[2] by other bees
Abronia maritima (sticky sand verbena)	N	+
Abronia umbellata (beach sand verbena)	N	+
Achillea millefolium (yarrow)	N	–
Althea rosea (hollyhock)	I	+
Amsinckia sp. (fiddleneck)	N	–
Anagalis arvensis (pimpernel)	I	–
Anemopsis californica (yerba mansa)	I	+
Antirrhinum nuttallianum (snapdragon)	N	+
Baccharis plumerae (Plummer's baccharis)	N	+
Bloomeria crocea (golden stars)	N	+
Brickellia californica (brickell bush)	N	–
Calochortus catalinae (Catalina mariposa)	N	++
Calochortus luteus (yellow mariposa)	N	++
Camissonia cheiranthifolia (beach primrose)	N	+
Camissonia micrantha (small-primrose)	N	–
Carpobrotus sp. (ice plant)	I	+
Castilleja sp. (Indian paintbrush)	N	–
Centranthus ruber (red valerian)	I	–
Cercocarpus betuloides (mountain mahogany)	N	++
Chorizanthe sp. (spineflower)	N	–
Clarkia purpurea (purple godetia)	N	–
Claytonia perfoliata (miner's lettuce)	N	–
Collinsia heterophylla (Chinese houses)	N	–
Conium maculatum (poison hemlock)	I	–
Convolvulus arvensis (bindweed)	I	++
Coreopsis gigantea (giant coreopsis)	N	++
Cotula coronopifolia (brass buttons)	I	–
Delphinium parryi (larkspur)	N	+
Dendromecon rigida (bush poppy)	N	+
Dichelostemma pulchellum (blue dicks)	N	–
Dodecatheon clevelandii (shooting star)	N	–
Dudleya candelabrum (live forever)	EL	++
Encelia californica (bush sunflower)	N	+

Appendix 3 (continued).

Flowers	Status[1]	Visited[2] by other bees
Eriogonum giganteum (St. Cathrine's lace)	I	+
Eriophyllum confertiflorum (golden yarrow)	N	+
Frankenia salina (alkali-heath)	N	+
Gnaphalium sp. (everlasting)	N	++
Haplopappus squarrosus (sawtooth goldenbush)	N	++
Haplopappus venetus (coastal goldenbush)	N	++
Heliotropium curassavicum (heliotrope)	N	+
Hemizonia fasciculata (common tarweed)	N	++
Hemizonia fitchii (spikeweed)	I	+
Hypochoeris glabra (smooth cat's ear)	I	+
Lasthenia californica (goldfields)	N	+++
Lathyrus laetiflorus (wild sweet pea)	N	++
Lavatera cretica (tree mallow)	I	–
Layia platyglossa (tidytips)	N	+
Lilium humboldtii (Humboldt lily)	N	–
Lomatium sp. (lomatium)	N	–
Lotus agrophyllus (silver lotus)	E	–
Lotus purshianus (Spanish clover)	N	++
Lotus strigosus (bishop's lotus)	N	–
Lupinus albifrons (silver lupine)	N	++
Lupinus spp. (lupine)	N	++
Marah sp. (wild-cucumber)	N	–
Medicago sativa (alfalfa)	I	–
Mesembryanthemum crystallinum (crystalline iceplant)	I	+
Mesembryanthemum nodiflorum (small-flowered iceplant)	I	+
Melilotus indicus (yellow sweet-clover)	I	–
Mimulus cardinalis (scarlet monkeyflower)	N	–
Mimulus flemingii (island monkeyflower)	E	–
Mimulus guttatus (common monkeyflower)	N	–
Nasturtium officinale (water cress)	I	–
Oenothera hookeri (Hooker's evening primrose)	N	++
Opuntia littoralis (prickly pear cactus)	N	++

Appendix 3 (continued).

Flowers	Status[1]	Visited[2] by other bees
Opuntia prolifera (coastal cholla)	N	+
Orthocarpus densiflorus (owl's clover)	N	–
Orthocarpus purpurascens (owl's clover)	N	–
Platystemon californicus (cream cups)	N	–
Rafinesquia californica (California chicory)	N	–
Ranunculus californicus (California buttercup)	N	++
Raphanus sativus (wild raddish)	I	–
Rhamnus californica (coffeeberry)	N	–
Rosa californica (wild rose)	N	–
Salix sp. (willow)	N	+
Sanicula sp. (snakeroot)	N	+
Senecio vulgaris (common groundsel)	I	–
Sidalcea malviflora (checker bloom)	N	+
Silene gallica (windmill pink)	I	+
Silene laciniata (Indian pink)	N	+
Solanum sp. (nightshade)	N	+
Solanum douglasii (Douglas' nightshade)	N	+
Solidago californica (California goldenrod)	N	–
Sonchus oleraceus (common sow-thistle)	I	+
Spergularia sp. (sand spurrey)	I	+++
Stachys bullata (wood-mint)	N	++
Trifolium sp. (clover)	N	–
Vanegasia carpesioides (canyon sunflower)	N	–
Verbascum thapsus (common mullein)	I	–
Verbena sp. (verbena)	N	++
Veronica americana (brook lime)	N	+
Vicia sp. (vetch)	N	–
Vinca major (periwinkle)	I	–
Viola pedunculata (Johnny jump-up)	N	–
Zauschneria californica (California fuchsia)	N	+
Zauschneria cana (fucshia)	N	+
Zigadenus fremontii (chaparral zygadene)	N	–

[1] **E** = endemic; **EE** = Santa Cruz Island only; **L** = listed; **N** = native; **I** = introduced.
[2] + = lowest visitation; +++ = highest visitation; – = not visited by other bees.