

Specialist Bee Pollinators of Showy Vernal Pool Flowers

ROBBIN W. THORP

Department of Entomology, University of California, Davis, CA 95616
(rwthorp@ucdavis.edu)

JOAN M. LEONG

Department of Entomology, University of California, Davis, CA 95616

CURRENT ADDRESS. Department of Science and Mathematics, University of Minnesota,
Morris, MN 56267

ABSTRACT. Bees of the family Andrenidae often specialize on a narrow range of flowering plants as pollen sources. This host specificity for pollen (oligolecty) involves close synchrony in space and time between the bees and their host plants. Plants of four genera, *Blennosperma*, *Downingia*, *Lasthenia*, and *Limnanthes*, produce showy floral displays often considered characteristic of California vernal pools and the pollinator guilds of each contain oligolectic andrenid bees that are likely to contribute significantly to plant reproduction. These bees nest in the uplands and forage for pollen from plants growing in the pools, thus ecologically linking the uplands and vernal pools together. In this paper we update several aspects of the biology of the andrenid bees that are oligolectic on vernal pool plants. The geographic distributions of these bees are within, but do not totally cover the geographic distributions of their pollen host-plant genera. The lack of geographic congruence may in part be due to our incomplete knowledge of the systematics of the bees. In preliminary transplant studies, adult bees were refrigerated for sufficient time for transport to and release at another site and mark-recapture of foraging females indicated that some colonization had occurred at the new site. Preliminary lists of floral visitor guilds of the four plant genera include many generalist bees and other insects in addition to the oligolectic bees. Many generalist flower visitors also live and nest outside the margins of the pools. Interactions between upland and pool biota have important implications for vernal pool conservation. To restore or create new pools as mitigation for destruction of existing pools, suitable habitat for flower visitors must also be restored or provided if we hope to have viable, long lasting vernal pool communities.

CITATION. Pages 169-179 in: C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr., and R. Ornduff (Editors). Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA. 1998.

INTRODUCTION

California vernal pool ecosystems are often characterized by populations of annual plants that bloom in the early spring. These plants have common names such as Yellow Carpet (*Blennosperma*), Meadowfoam (*Limnanthes*), Goldfield (*Lasthenia*), and Skyblue (*Downingia*), that elegantly describe their showy displays of dense and abundant flowers. Many solitary bees of the family Andrenidae specialize on these flowering taxa for collecting pollen and in some areas may be their principal pollinators (Thorp, 1990). For example, Leong (1994) in her studies of *Blennosperma nanum* (Hook.) S. F. Blake var. *nanum* at Jepson Prairie Preserve suggests that its oligolectic, *Andrena* (*Diandrena*) *blennospermatis* Thorp, can be the predominant visitor.

While these specialist bees forage in the flora-rich pool basins, they nest in the upland areas near the vernal pools. Therefore, they link the lower lying aquatic with the upland terrestrial microhabitats within the vernal pool ecosystem. Since these bees are likely to be important in the reproduction of many vernal pool plant species, the quality of upland habitat needs to be considered in addition to vernal pools proper when evaluating the viability of created and/or restored vernal pool habitats.

Mitigation projects for loss of vernal pools may involve creation of pools in new areas some distance from the original pools. Seeds of vernal pool plants, and eggs and cysts of invertebrates of special concern can easily be obtained by vacuuming or carefully removing surface materials from dried pool areas. This matter from pools to be destroyed can be used to inoculate newly created pools. If the hydrologic conditions are adequate, the addition of water in the form of winter rains should

METHODS

Geographic distributions

suffice to initiate germination and development of seeds, eggs, and cysts in the created pools. Specialist (= oligolectic) bees may colonize the new site if the upland habitat is suitable for their nesting requirements. This is best facilitated if newly created pools are on-site and if the original upland habitats are leveled or destroyed well after the time the flowering plants bloom and native specialist bees emerge. If these conditions are not met, the plants will be forced to rely upon generalist pollinators already established in the new habitat to pollinate their flowers.

The general life cycles and floral associations of vernal pool oligolectic bees have been discussed in previous papers (Thorp, 1969; 1976; 1990; Rust, 1976; Leong, 1994; Leong et al., 1995; Thorp and Leong, 1995) and will only be summarized here. The vernal pool oligolectes discussed in this paper are all members of the bee family, Andrenidae. They are solitary, ground nesting bees. They have only one generation per year, like their pollen host plants. Adult activities (mating, nest construction, foraging, brood cell provisioning, and egg laying) are limited primarily to the bloom period of their pollen host plants. Most of the annual life cycle of the bees is spent underground as immatures in the brood cell, feeding and growing as larvae in spring, resting through the summer as post-defecating larvae followed by a brief spurt of pupation in early autumn, and finally resting overwinter as adults in their natal cells. In this way they are ready to emerge quickly as the spring bloom of their pollen host plants begin. The males tend to emerge first (protandry) and mating occurs with or just before initial bloom. Females construct shallow nests in upland soils in the vicinity of host plant populations. These oligolectic bees are K-selected in contrast to most insect species, in that they produce very few offspring per female (ca <30), but invest heavily in provisioning for their young. Where present, they often tend to be the most abundant visitors in the guilds of potential pollinators of their pollen host plants. Females tend to return to the same flower patches during successive foraging bouts and to forage over restricted areas, usually visiting a near-neighbor of the flower previously visited, which restricts gene flow that occurs via pollen dispersal.

Our primary focus here is to provide a summary of our current understanding of the geographic distributions of oligolectic bees in relation to their pollen host plants in vernal pool habitats, and to document the guilds of specialist and generalist flower visitors, with emphasis on outcrossing vernal pool species of the genera *Blennosperma*, *Lasthenia*, *Downingia*, and *Limnanthes*. As gaps in our knowledge of these bees exist, we also discuss potential difficulties associated with their poorly documented geographic distributions. Additionally, we report results of preliminary field tests that were conducted to evaluate the potential for transplanting oligolectic bees to newly created vernal pool habitats for mitigation projects.

Field data on the ecology and systematics of vernal pool plant pollinators have been accumulated by one of us (RWT) on a casual basis since about 1960, with periods of intensive field studies in the 1970's, and by both of us in the 1990's as funding has become available. Species of principal interest have been oligolectic (pollen host specific) bees of the genus *Andrena* including: *A. (Diandrena) blennospermatis* Thorp, *A. (D.) submoesta* Viereck, and *A. (D.) puthua* (Cockerell); *A. (Hesperandrena) limnanthis* Timberlake, *A. (H.) duboisi* Timberlake, *A. (H.) lativentris* Timberlake and other undescribed species (Thorp, 1969; 1976; 1990; Thorp and Leong, 1995; Leong, 1994; Leong et al., 1995). Also of interest were *Panurginus occidentalis* (Crawford), and *P. atriceps* (Cresson) (Rust, 1976; Thorp, 1976; 1990).

Distributions of specialist bees relative to their pollen host plant taxa presented herein are based on our own field collections, other museum specimens, and literature records. Maps of the currently known distributions of major oligolectic bee species have been constructed and superimposed on the currently known distributions of their pollen host taxa according to the most recent revisions of: *Blennosperma* (Ornduff, 1964); *Downingia* (Weiler, 1962); *Lasthenia* (Ornduff, 1966); and *Limnanthes* (Mason, 1952).

Transplantation

Due to the potential importance of oligolectic bees to the reproduction of their pollen host plants, the desirability for transplanting oligolectic bees to new habitats was explored. Nests of these andrenids are not easy to locate. Adult females after they emerge, mate, establish nests, and begin foraging are the easiest stage to collect. Therefore, emphasis was placed on two aspects of transplanting female bees. First we tested the survival and longevity ("shelf life") of bees kept under cold storage for transportation between sites and secondly we performed a mark-release-recapture study of transplanted females.

Cold storage survival. Twenty-one female bees were collected while foraging for pollen at host flowers at several sites: Merced Co. on *Downingia* (6); Sonoma County on *Downingia* (6); Solano County on *Downingia* (2) and on *Lasthenia* (7). They were transferred to small plastic vials containing some of the host flowers. The vials were placed in a cooler with blue ice and returned to the Davis campus. The vials were then stored in a refrigerator at about 4°C. The vials were removed periodically and brought to room temperature (ca 25°C) to check for mortality. Specimens were categorized as: "Alive" if they were able to right themselves and actively crawl around the vial; "Twitching" if there was any perceptible movement of legs or

antennae after 10 minutes warming; or “Dead” if no movement or response to probing after 10 minutes warming. Dead bees were removed and pinned as vouchers. Most alive bees became active within a couple of minutes at room temperature. Bees that were alive or exhibited some twitching response were returned to refrigeration. These observations continued for up to 4 weeks.

Mark-recapture study. This involved capture of 91 nesting *Andrena* females while they were gathering pollen from *Lasthenia* south of Olcott Lake, Jepson Prairie Preserve, Solano County, CA on 18 April 1994. The females were transferred to plastic vials and placed in an ice chest on blue ice. They were transported to Davis. That evening they were categorized by size, identified, and marked with an orange paint spot on the middle of the thoracic dorsum and placed in 10.5x5.5x2.5 cm cardboard slide boxes. The next morning (07:35 am) they were transported on ice and released at the same Preserve in an area with good bloom of *Lasthenia*, but about one mile north of the capture site (to minimize the chances of the bees returning to their original foraging site). The slide boxes containing the bees were placed on a larger cardboard box weighted with rocks to prevent being blown over. The slide boxes were opened partially so that the bees could escape and yet be protected from bird predation while still groggy. As soon as the boxes were opened, bees began crawling out and up their sides. The boxes were first checked that afternoon (13:05 pm) to evaluate the success of release. Subsequent surveys to determine the presence of the marked bees at the release site and at the site of original capture one mile south were made three and eight days after release. Bees were netted at flowers, examined for the mark, and released.

Flower Visitor Guilds

Our field collections provide us with data to document guilds of potential pollinators of the four major showy vernal pool flowering taxa. We have examined these to determine the specialist and generalist visitors to the various vernal pool plant taxa. Sampling/monitoring flower visitor guilds primarily involved field collection by insect nets, accompanied by visual observations; this was more recently augmented by pan-trap sampling (Leong and Thorp, 1995).

RESULTS

Geographic Distributions

The geographic distributions of specialist bees tend to be well within the ranges of their pollen host plant genera, and tend to conform most closely to distributions of their outcrossing host species (Figures 1-4). For example, *Panurginus occidentalis* and *Andrena limnanthis* are found throughout most of the ranges of *Limnanthes douglasii*, *L. alba*, *L. montana*, *L. striata*, and the

endangered *L. vinculans*, all outcrossing species. However, they have not been found in association with *L. douglasii* ssp. *sulphurea* at Point Reyes National Seashore. They occur with *L. floccosa*, a selfer, only where it is sympatric with *L. alba* and are not found with the selfing populations of *L. gracilis* in southern Oregon or in San Diego County, California.

***Blennosperma*.** New distribution records of *Andrena* (*Diandrena*) *blennospermatis* Thorp (Figure 1) more than double the area of distribution as published by Thorp (1969). However, it covers only a small (northern) portion of the distribution of *Blennosperma nanum* var. *nanum*. One of us (RWT) has briefly sampled populations of *Blennosperma nanum* in Butte County (east of Durham) and Fresno County (Ford Table) without finding the *Diandrena* oligolege. Females of this bee collect pollen from both *B. nanum* var. *nanum* and the endangered *B. bakeri*. [See note added in proof.]

***Lasthenia*.** New geographical records of *Andrena* (*Diandrena*) *submoesta* Viereck and *A. (D.) puthua* (Cockerell) fill some gaps, but do not greatly extend the distribution records published by Thorp (1969) (Figure 2, Appendix I). These two species of *Diandrena* collect pollen only from flowers of the genus

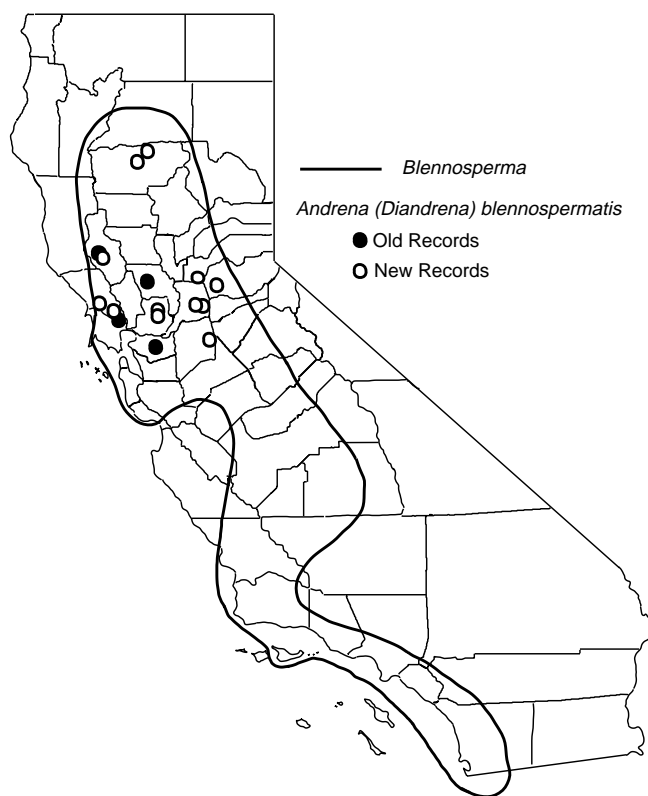


FIGURE 1. Geographic distribution of the outcrossing species of *Blennosperma* (bounded by the black line) and its oligolege, *Andrena* (*Diandrena*) *blennospermatis* (closed circles are records published by Thorp (1969), open circles are new records).

Lasthenia. They overlap considerably in space and time and share floral resources (Thorp, 1969). Their distribution areas cover most of the central range of the genus *Lasthenia*, especially of the widespread *L. californica*. *A. puthua* is more prominent in the Transverse Ranges of southern California and extends further south into Baja California, while *A. submoesta* is more prominent north of the San Francisco Bay area and in the southern Sacramento Valley (Figure 2).

Most species of *Hesperandrena*, especially *A. (H.) baeriae* Timberlake, *A. (H.) duboisi* Timberlake, *A. (H.) lativentris* Timberlake, and several undescribed species, collect pollen from flowers of *Lasthenia*. Some overlap in space and time and share the same floral resource both with each other and with *A. (Diandrena) submoesta* and *A. (D.) puthua* (Figure 2).

Limnanthes. The distribution of *Panurginus occidentalis* (Crawford), an oligolege of *Limnanthes*, tends to be quite similar to that of *A. (Hesperandrena) limnanthis* and frequently the two occur sympatrically (Figure 3, Appendix I). Females of

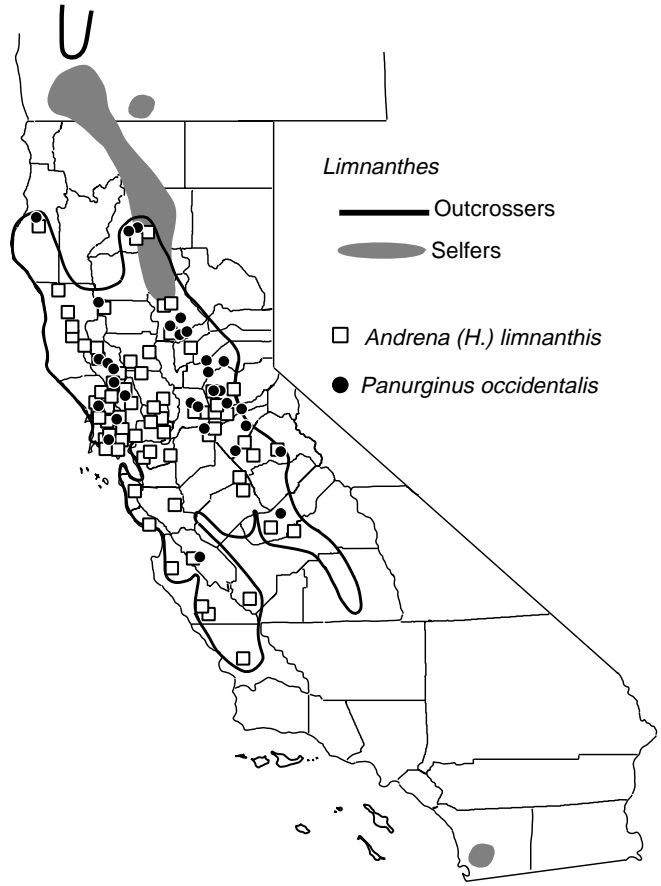


FIGURE 3. Geographic distribution of *Limnanthes* (gray areas are selfing species, black line bounds outcrossers) and its oligolegic bees: *Andrena (Hesperandrena) limnanthis* (open squares) and *Panurginus occidentalis* (closed circles).

these bees collect pollen primarily from *L. douglasii* subspecies *douglasii*, *nivea*, and *rosea*, and to a lesser degree from *L. alba*, *L. montana*, *L. striata*, and the endangered *L. vinculans*.

Downingia. The known distribution of *Panurginus atriceps* (Cresson), the putative oligolege of *Downingia*, is based entirely on our own collections on the host plant, since there is confusion over the correct nomenclature of this bee species as judged by examinations of determined specimens in museum collections. Our current validated records for the bee flower relationship are well within the generic distribution of *Downingia* (Figure 4). Females of this bee collect pollen primarily from outcrossing species that have a short anther tube: *D. bicornuta*, *D. concolor*, *D. cuspidata*, *D. ornatissima*, and *D. pulchella*.

Specific locality records for all these oligolegic bees are given in Appendix I. For the three species of *Diandrena*, only new records since Thorp (1969) are listed.

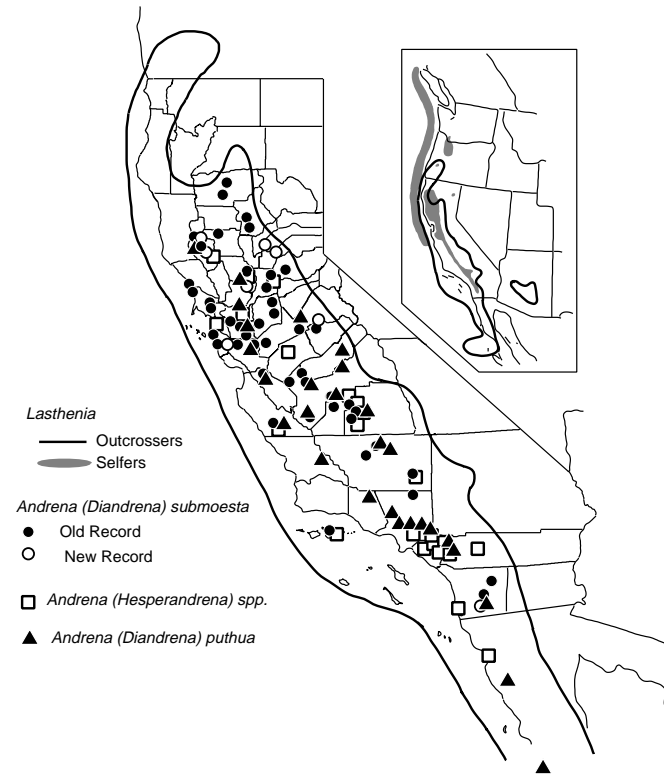


FIGURE 2. Geographic distribution of *Lasthenia* in North America (selfing and outcrossing species shown on inset, solid line encloses outcrossers) and its oligolegic bees: *Andrena (Diandrena) submoesta* (closed circles are records published by Thorp 1969, open circles are new records), *A. (D.) puthua* (solid triangles) and *A. (Hesperandrena) spp.* (including: *A. baeriae*, *A. duboisi*, *A. lativentris* and several undescribed species, open squares).

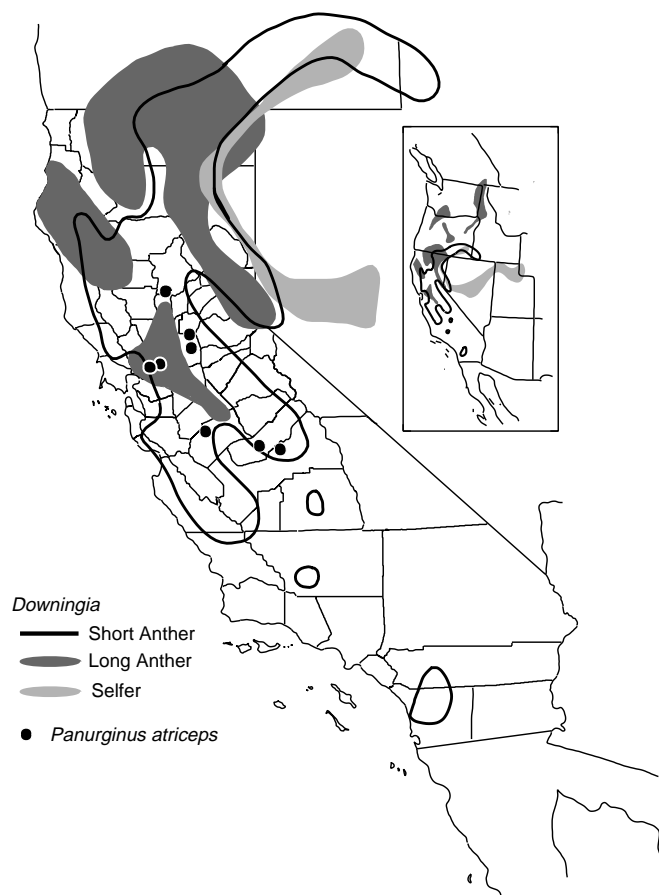


FIGURE 4. Geographic distribution of the North American species of *Downingia* (gray grid = selter; black = outcrossing species with long anther tubes; black line bounds outcrossers with short anther tubes) and their oligolege, *Panurginus atriceps* (closed circles).

Transplantation

In studies to test the feasibility of transplanting foraging female oligolectic bees, considerable variation was shown in survivorship of bees stored under refrigeration in the laboratory. Some mortality occurred within the first two days, but 66.7% of the 21 bees were alive after one week and nearly 43% of the bees were still alive after two weeks of storage. Maximum length of survival in cold storage was 26 days.

In the mark-recapture study, 91 marked bees were returned the next morning to Jepson Prairie Preserve and released one mile north of the site of their capture. Five marked bees were found dead in the release boxes 5.5 hours after release; no dead bees were found in the vicinity of the release box. Thus, we assume that 86 marked bees were released. No marked bees were recaptured on the day of release among 132 bees sampled at the release site and 75 at the original collection site. Three days after release, one marked bee out of 37 bees surveyed was ob-

served collecting pollen at *Lasthenia* at the release site. By the 8th day, when most of the *Lasthenia* flower heads were spent, 12 bees were observed at the release site, but none were marked.

Flower Visitor Guilds

Guilds of both specialist and generalist bees and other generalist visitors tend to be most diverse in association with *Lasthenia* and *Limnanthes* and least diverse in association with *Blennosperma* and *Downingia* (Appendix II). The greatest number of oligolectic species, including complexes of sympatric, and thus potentially competing species, are also associated with *Lasthenia*. Within the genus *Limnanthes*, the most diverse generalist visitor guilds are associated with *L. douglasii* ssp. *sulphurea* and *L. striata*.

Our lists record all species observed and do not distinguish rare versus common occurrences nor visit frequencies by each visitor species. Individuals of the oligolectic bee species are often the most abundant flower visitors, followed by generalist bees, flies of the families Anthomyiidae, Bombyliidae, Syrphidae, and Empididae, and pollen feeding beetles of the families Dasytidae, Melyridae, and Dermestidae. Although they may obtain part of their food resources from vernal pool flowers, none of these generalist guild members are restricted to vernal pool habitats.

DISCUSSION

In general, geographic distributions of oligolectic bees that pollinate showy vernal pool flowers tend to be well within the central part of the ranges of the outcrossing species of their pollen host plant genera (Figures 1-4). These bees collect pollen only from plants of their preferred hosts. They are not restricted to single host plant species, but they do not visit all species in their host genera. However, our knowledge of their geographic distributions in vernal pool habitats remains incomplete.

Blennosperma blooms earliest (February-March), when the weather is rainy and least conducive for entomologists to be collecting. The fact that we were able to double the distribution records for *A. blennospermatis* suggests that the limits of its distribution are yet to be established. *Lasthenia* and *Limnanthes* both attract the greatest diversity of visitors (Appendix II) and bloom during a time when weather is sunnier and entomologists are more likely to be in the field. *Downingia* attracts relatively fewer visitors due to its specialized flower form; and being a small "belly flower" does not attract the attention of many entomologists. Thus, our knowledge of geographic distributions of oligolectic bees in vernal pool habitats is probably most complete for bees associated with *Lasthenia* and *Limnanthes*.

The incomplete nature of many of our distribution records is in part also due to our insufficient knowledge of the systematics of the bee taxa. Identification of oligolectic bees in vernal pool habitats is problematic for many species due to insufficient systematic literature. Only for *Andrena* (*Diandrena*) is there a systematic revision with keys, descriptions, ecological data, and distribution records to identify the bees (Thorp, 1969). And even in this subgenus, we were able to make some significant additions to the distribution records of the vernal pool species. The paucity of information is illustrated by the two oligolectes of *Limnanthes*. *Andrena* (*Hesperandrena*) *limnanthis* and *Panurginus occidentalis* are the most distinctive and recognizable in their respective taxa, but detailed information on distribution records to augment our own field collections had to be ferreted out from mostly undetermined material in museum collections. Until further field associations are made and a revision of the genus *Panurginus* is completed, the nomenclature, distribution, and floral specificity of the principal pollinator of *Downingia* will remain an enigma. At this juncture, it appears that the species currently referred to as *P. atriceps* is actually a complex of at least two species (Thorp unpublished data): a widespread species that visits *Ceanothus* and other chaparral shrubs (Dobson, 1993) and another that visits only *Downingia* (Rust, 1976). There are also several undescribed species of *Andrena* (*Hesperandrena*) associated with *Lasthenia* and a revision of the subgenus is needed before they can be identified or studied with certainty.

Our limited experiments have demonstrated some potential for transplanting specialist bees. Field-collected foraging females that had mated and established initial nests could be held under refrigeration for up to one week with 66.7% survival. This is sufficient time to transport and release them at distant sites, and to allow for several days of inclement weather that would delay bee releases. Of course, in any attempts to transplant adult bees, it is important to determine the success of colonization after release. Bees should be marked for ease of identification after release. Even if nests cannot be located, the occurrence of marked females collecting pollen on their host plants is a good indication that they have established nests in the release area.

In our transplantation studies, we selected foraging females that had established nests, because of availability and ease of collection. Transplantation of freshly emerged adult bees, both males and females, may yield higher colonization success, since the primary time for dispersal to new habitats is likely to be prior to the time of mating, nest establishment, and initiation of pollen foraging. Successful colonization would then depend on the suitability of the new site in providing proper resources such as pollen host plants and nesting habitat. However, the window of opportunity to collect these freshly emerged bees is very small. Another approach is to transplant progeny in their brood nests. We have not yet explored methods for this, but difficulties could arise from the fact that these bees tend not to be highly

gregarious making it rare to find groups of more than 12 nests in a nest site area. If sufficient nests could be located, they might be excavated during the summer when the larvae are resting after having completed their feeding, or in the autumn/winter when they have pupated and are in the overwinter resting adult stage. In either case, methods would need to be devised for transplanting soil cores for temporary storage prior to transplanting to ensure that the brood cells remained intact and were not physically damaged. Methods for successfully transplanting progeny in soil nests have been developed for the solitary, but highly gregarious nests of the alkali bee, *Nomia melanderi* Cockerell, (Stephen, 1960).

At best, transplanting these oligolectic ground nesting bees either as immatures or as emerged adults, is a challenging endeavor. Availability of adequate numbers of bees, narrow windows of time suitable for bee collection and/or transfer, and the likelihood that the bees may leave the release site if not all conditions are perceived as suitable compound the difficulty. Also, since vernal pool habitats contain other specialist and many generalist bees, accurate identification of desired target species for transplantation is important. Accurate identification or confirmation of initial identifications of most of these bees will require the aid of an expert. These bees are especially difficult to identify in the field. Collection of samples for examination and comparison with collections in a museum is usually required and voucher specimens should be deposited in a public entomology museum. There are published keys to the genera of bees (Michener et al., 1994), the subgenera of *Andrena* (LaBerge, 1986), and the species of *Diandrena* (Thorp, 1969). However, the latter two are difficult for the inexperienced to use. There are no keys available for *Andrena* (*Hesperandrena*) or *Panurginus* and since neither of these taxa have been revised they contain many undescribed species.

Although our focus here is on oligolectic bees, the guilds of visitors to the major showy vernal pool flower genera are diverse and usually contain many species of generalist bees, flies, and beetles in addition to oligolectic bees. The visitor guilds of *Blennosperma* and *Downingia* exhibit the least diversity. *Blennosperma* is the earliest blooming when fewer insect species are available. *Downingia*, although the latest blooming species, has the most specialized flower morphology. Visitor guilds of *Limnanthes* and especially *Lasthenia* show the greatest diversity of floral visitors. *Lasthenia* also has greatest number of oligolectes, including many sympatric species, as members of its visitor guilds. Our lists of guild memberships are biased in that each taxon is represented equally based on an occurrence without regard to the relative frequencies or abundances of individuals in each taxon. Therefore a species with only one record may appear equal to one with many individual records, from different times and localities. The lists also do not indicate the quality of the floral visit, e.g., whether the insects forage for

pollen and/or nectar or visit the flower for some more casual reason. They are meant to serve as a starting place for future studies, such as investigations of the relative pollination efficiencies of different guild members. It is crucial to establish which guild members are the main pollinators. Presence of key pollinators should be an important consideration in vernal pool habitat conservation efforts.

In summary, we know a fair bit about the specificity and seasonal synchrony of the oligolectic andrenid bees to their vernal pool pollen host-plant taxa, as well as about their annual life cycles. However, our information on their systematics (except for *Diandrena*), dispersal, nesting habitat requirements, and distributions relative to their host plants is limited and needs more attention for us to understand their role in the reproductive biology of vernal pool plants. Some particularly interesting questions that need to be addressed include: What happens to plant reproduction in areas beyond the distribution ranges of their oligolectes? Are each of the oligolectic bees the most important pollinators of their pollen host plants? If so, how do we save them and possibly transplant them to restoration/creation sites for mitigation? Furthermore, a question not often asked is are these oligolectic bees worth conserving for their own sakes? We would answer the last with a firm yes. These bees are "inhabitants" and not merely "passers through" to paraphrase M. G. Barbour, keynote speaker of this symposium. They are totally dependent on the pollen from their specific host plant genera for the production of their progeny and thus for their survival. Their populations will become extinct wherever vernal pools containing their pollen host plants and/or their upland nesting habitats are destroyed. And plants that depend on these bees for their reproduction may also decline.

Preservation of existing vernal pool habitats is the most preferable type of mitigation for loss of vernal pool habitat as long as the complex biological interactions, processes, and functions are still intact. Restoration of vernal pools is less effective, being limited by the quality of the remaining habitat values, including uplands, and our ability to recognize and successfully restore those that have been degraded or lost. Creation of vernal pools is a very challenging approach and is one that also requires consideration of surrounding upland habitat for its value as nesting sites for bees, both oligolectes and generalists, that pollinate many showy vernal pool flowers. Conservation of the interaction of pollinators with vernal pool flowers is important for maintaining the long-term viability of these plants, especially the showy outcrossing taxa.

ACKNOWLEDGMENTS

Part of this research was sponsored by grants from DOT (CalTrans) to RWT [RTA-65T133] and to JML [RTA-65T188] and we wish to thank Jeff Gidley and Harold Hunt, CalTrans Biologists, Sacramento Office for their advice and support. We

also thank cooperators who provided us access to vernal pool habitats and mitigation pools including: Dr. John Stebbins and Bill Traylor, CSU Fresno, and Bob Epperson, CalTrans Biologist, Fresno Office; Dr. Phil Northen and Doug Eakins, CSU Sonoma; and Neila Stewart, Environmental Coordinator, City of Roseville. Early research on pollination of *Limnanthes* was sponsored by a grant from the Institute of Ecology, University of California, Davis [OPER #4781] to RWT and Dr. Subodh Jain. We also wish to thank cooperators who helped collect and make field observations on vernal pool flower visitor guilds over many years including: Dennis Briggs; Drs. James Estes, Heidi Dobson, and Carll Goodpasture. Vouchers of our field collections are deposited in the R. M. Bohart Museum of Entomology, University of California, Davis. Special thanks to Dr. David M. Gordon for preparation of the distribution maps.

NOTE ADDED IN PROOF

On 14 March 1997, Carol Witham and Greg Kareofelas extended the range of *Andrena (Diandrena) blennospermatis* over 100 miles northward from Lake County to Tehama County. They collected females of this bee on *Blennosperma nanum* in the vicinity of Red Bluff. These confirm our contention in the discussion that the limits of the distribution of this bee are yet to be established.

LITERATURE CITED

- Dobson, H.E.M. 1993. Bee fauna associated with shrubs in two California chaparral communities. *Pan-Pacific Entomologist* 69(1):77-94.
- LaBerge, W.E. 1986. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part XI. Minor subgenera and subgeneric key. *Transactions of the American Entomological Society* 111:441-567.
- Leong, J.M. 1994. Pollination of a patchily-distributed plant, *Blennosperma nanum*, in natural and artificially created vernal pool habitats. Ph.D. Dissertation, University of California, Davis, CA.
- Leong, J.M., R.P. Randolph, and R.W. Thorp. 1995. Observations of the foraging patterns of *Andrena (Diandrena) blennospermatis* Thorp (Hymenoptera: Andrenidae). *Pan-Pacific Entomologist* 71(1):68-71.
- Leong, J.M. and R.W. Thorp. 1995. Pan traps and oligolectic bees: An alternative sampling method using the color preferences of specialist bee pollinators. *International Society of Hymenopterists, Third Annual Conference. UC Davis. August 12-17, 1995. Abstracts of Papers and Posters, p. 17.*
- Mason, C.T., Jr. 1952. A systematic study of the genus *Limnanthes* R. Br. *University of California Publications in Botany* 25(6):455-512.
- Michener, C.D., R.J. McGinley, and B.N. Danforth. 1994. The bee genera of North and Central America (Hymenoptera: Apoidea). *Smithsonian Inst. Press, 209 pp.*
- Ornduff, R. 1964. Biosystematics of *Blennosperma* (Compositae). *Brittonia* 16:289-295.

- Ornduff, R. 1966. A biosystematic survey of the goldfield genus *Lasthenia* (Compositae: Helenieae). University of California Publications in Botany 40:1-92.
- Rust, R.W. 1976. Notes on the biology of North American species of *Panurginus* (Hymenoptera: Andrenidae). Pan-Pacific Entomologist 52(2):159-166.
- Stephen, W.P. 1960. Artificial beds for the propagation of the alkali bee, *Nomia melanderi* Ckll. Journal of Economic Entomology 53:1025-1030.
- Thorp, R.W. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). University of California Publications in Entomology 52:1-146.
- Thorp, R.W. 1976. Insect pollination of vernal pool flowers. Pages 36-40 in: S. Jain (Editor). Vernal pools, their ecology and conservation. Institute of Ecology Publication No. 9, University of California, Davis, CA.
- Thorp, R.W. 1990. Vernal pool flowers and host specific bees. Pages 109-122 in: D.H. Ikeda and R. A. Schlising (Editors). Vernal Pool Plants – Their Habitat and Biology. Studies from the Herbarium No. 8, California State University, Chico, CA.
- Thorp, R.W. and J. M. Leong. 1995. Native bee pollinators of vernal pool plants. Fremontia 23(2):3-7.
- Weiler, J.H. 1962. A biosystematic study of the genus *Downingia*. Ph.D. dissertation, Univ. California, Berkeley, CA.

SPECIALIST BEE POLLINATORS OF SHOWY VERNAL POOL FLOWERS

APPENDIX I. Distribution records of andrenid bees oligolectic on vernal pool flowers [for *Andrena* (*Diandrena*) spp., only new records not listed in Thorp (1969)]:

Andrena (*Diandrena*) *blennospermatis*:

CA: *El Dorado Co.*: Bass Lake, 6 mi WSW Rescue. *Lake Co.*: Finley, 2 mi NW. *Sacramento Co.*: Bridgehouse, 2 mi W; Slough House, 4 mi E. *San Joaquin Co.*: Bellota, 2 mi E. *Solano Co.*: Dixon, 8 mi S; Dozier, 11 mi S Dixon (= Jepson Prairie Preserve). *Sonoma Co.*: Santa Rosa, Alton Rd.; Sebastopol, 4 mi ESE. *Tehama Co.*: Red Bluff, 3 mi E and 13 mi NNE.

Andrena (*Diandrena*) *puhua*:

CA: *San Diego Co.*: Transect 1970-72: Descanso-Alpine site. *Solano Co.*: Dixon, 11 mi S (= Jepson Prairie Preserve).

Andrena (*Diandrena*) *submoesta*:

CA: *Butte Co.*: Biggs, 6 mi NNE; Chico, 10 mi SE. *Colusa Co.*: Bear Creek; Bear Valley, 8.8 mi N Hwy 29. *El Dorado Co.*: Bass Lake, 6 mi, WSW Rescue. *Fresno Co.*: Ford Table, 10 mi, ENE Friant. *Lake Co.*: Kelseyville, 5 mi SE; Lower Lake, 5.5 mi W. *Placer Co.*: Roseville. *Sacramento Co.*: Folsom, 6.5 mi S; Mather AFB; Slough House, 4 mi E. *San Diego Co.*: Transect 1970-72: Descanso-Alpine site. *San Joaquin Co.*: Bellota, 2 mi E; Clements, 7 mi NE. *San Mateo Co.*: Stanford Campus Expt. Area. *Santa Barbara Co.*: Santa Cruz Island. *Solano Co.*: Dixon, 11 mi S (= Jepson Prairie Preserve). *Tehama Co.*: Corning, 5 mi W; Red Bluff. *Tuolumne Co.*: Groveland, 6 mi E. *Yuba Co.*: Beale AFB, 7 mi E Marysville.

Andrena (*Hesperandrena*) *limnanthis*:

CA: *Alameda Co.*: Oakland, (SE of). *Amador Co.*: Ione, (SW of); Plymouth, 5 mi SW. *Butte Co.*: Biggs (N of); Chico, 10 mi SE. *Calaveras Co.*: Angels Camp. *Colusa Co.*: Bear Valley, 9.7 mi N of Hwy 20; Colusa. *Contra Costa Co.*: Byron; Walnut Creek (W of). *El Dorado Co.*: Placerville; Shingle Springs. *Fresno Co.*: Coalinga, (ca 15 mi W); Ford Table, 10 mi ENE Friant. *Humboldt Co.*: Kneeland, (W of). *Lake Co.*: Finley (SE of); Lakeport (& NW & S); Lower Lake, 2 mi S; Middletown; Upper Lake (SE of). *Madera Co.*: Madera, 10 km ENE. *Marin Co.*: Fairfax; Pt. Reyes; San Geronimo. *Mendocino Co.*: Bell Springs; Laytonville; Potter Valley; Willits (& N of). *Monterey Co.*: Carmel Valley (W of); Jolon (W of & WNW of). *Napa Co.*: Calistoga (N of); Napa (S of); Pope Valley and vicinity. *Sacramento Co.*: Fair Oaks; Slough House, 2 and 4 mi E (& W of). *San Benito Co.*: Paicines (ca 11 mi S). *San Joaquin Co.*: Clements, 7 mi NE. *San Luis Obispo Co.*: Santa Margarita (ca 5 mi NW). *San Mateo Co.*: Menlo Park. *Santa Clara Co.*: Mt. Hamilton. *Santa Cruz Co.*: Felton. *Shasta Co.*: Ingot; Palo Cedro. *Solano Co.*: Dozier, 11 mi S. Dixon (= Jepson Prairie Preserve); Vacaville. *Sonoma Co.*: Agua Caliente; Forestville; Healdsburg (N of); Kenwood; Santa Rosa, Alton Rd site; Sebastopol, 4 mi ESE (& N of); Sonoma; Two Rock, 1 mi W and 2 mi N; Valley Ford and 1 mi N. *Stanislaus Co.*: Evergreen Rd, 3.2 mi W Hwy 120; La Grange (N of). *Tuolumne Co.*: Chinese Camp; Groveland; Mather, 3 and 4-5 mi S. *Yolo Co.*: Davis, 5 mi W; Rumsey; Winters. *Yuba Co.*: Beale AFB, 7 mi E Marysville.

Andrena (*Hesperandrena*) spp. (associated with *Lasthenia*):

MEX.: *Baja California*: Ensenada. CA: *Contra Costa Co.*: Mt. Diablo and Russleman Park; Walnut Creek. *Kern Co.*: Mojave. *Lake Co.*: Lower Lake, 5.5 mi W. *Los Angeles Co.*: Puente Hills nr. Whittier; Santa Catalina Island, Rancho Escondido. *Merced Co.*: San Luis National Wildlife Refuge, 10 mi N Los Banos. *Monterey Co.*: Lockwood, 1 mi. W. *Orange Co.*: Rancho Santa Ana. *Riverside Co.*: Albermill, 11.5 mi NW; Gavilan; Hemet Lake; Herkey Creek; Lake Mathews; Perris, 2, 3, and 4 mi W; Railroad Canyon; Riverside; Rosamond, Hills N of. *Sacramento Co.*: Bridgehouse, 2 mi W. *San Diego Co.*: San Diego. *San Francisco Co.*: San Francisco. *Santa Barbara Co.*: Santa Cruz Island. *Tulare Co.*: Earlimart; Goshen; Strathmore; Tipton, 10 mi W; Visalia. *Yolo Co.*: Davis.

Panurginus atriceps

CA: *Butte Co.*: Biggs, 6 mi NNE. *Fresno Co.*: Table Mtn. *Madera Co.*: USBR Equalization Reservoir site. *Merced Co.*: Grasslands State Park, 14.2 mi N Los Banos. *Placer Co.*: Roseville. *Sacramento Co.*: Mather AFB. *Solano Co.*: Dozier, 9 mi S Dixon; Dozier, 11 mi S Dixon (= Jepson Prairie Preserve); Travis AFB.

Panurginus occidentalis:

CA: *Amador Co.*: Fiddletown, 5.6 mi E; Pioneer; Plymouth, 5 mi SW; Volcano, 5.1 mi NE. *Butte Co.*: Bangor; Biggs (vic); Oroville, 7 mi NNE; Palermo-Horcutt Rd, 2.2 mi N Central House; Table Mtn. *Calaveras Co.*: Rt. 49, 1.9 mi S Angels Camp; Sheep Ranch. *El Dorado Co.*: Diamond Springs; Shingle Springs. *Humboldt Co.*: Kneeland, 15.6 mi S. *Lake Co.*: Finley, 2 mi W; Lower Lake (vic); Middletown; Rt. 29 & Rt. 175. *Madera Co.*: Coarsegold, 8 mi S. *Marin Co.*: Forest Knolls, 3.4 mi S. *Napa Co.*: Pope Valley, 3 mi N and 3 mi S. *Nevada Co.*: 1.8 mi N County line, Rd. 49. *Placer Co.*: Auburn; Foresthill, 5 mi W. *Sacramento Co.*: Mather AFB; Rt. 16, 1.5 mi W Eagles Nest Rd. *San Benito Co.*: Rt. 25, 0.3 mi N Glora Rd. *San Joaquin Co.*: Clements. *Shasta Co.*: Ingot; Palo Cedro. *Sonoma Co.*: Agua Caliente, 3 mi N; High School Rd. 0.3 mi S Occidental Rd.; Rt. 12, ca 12 mi N Sonoma. *Tuolumne Co.*: Groveland; Mather.

APPENDIX II. Flower Visitor Guilds of Showy Vernal Pool Plant Taxa. * denotes oligolectic bee species.

Blennosperma

HYMNENOPTERA

ANDRENIDAE

**Andrena (Diandrena) blennospermatidis*

A. (Hesperandrena) limnanthis

A. (Tylandrena) layiae

ANTHOPHORIDAE

Nomada spp.

Synhalonia sp.

APIDAE

Apis mellifera

HALICTIDAE

Dialictus sp.

Evyllaenus sp.

Halictus sp.

Lasioglossum sp.

Sphecodes sp.

MEGACHILIDAE

Osmia spp.

DIPTERA

ANTHOMYIIDAE

Scatophaga stercoraria

BOMBYLIIDAE

CALLIPHORIDAE

CONOPIDAE

Myopa sp.

EMPIDIDAE

EPHYDRIDAE

Rhamphomyia spp.

RHAGIONIDAE

SYRPHIDAE

COLEOPTERA

CANTHARIDAE

MELOIDAE

Meloe? sp.

Lasthenia

HYMNENOPTERA

ANDRENIDAE

**Andrena (Diandrena) submoesta*

**Andrena (Diandrena) puthua*

**Andrena (Hesperandrena) baeriae*

**Andrena (Hesperandrena) duboisi*

**Andrena (Hesperandrena) lativentris*

**Andrena (Hesperandrena) spp. (2-3 n. sp.)*

Andrena (Micrandrena) sp.

Andrena (Tylandrena) layiae

Panurginus sp.

ANTHOPHORIDAE

Nomada spp.

APIDAE

Apis mellifera

CHRYSIDIDAE

COLLETIDAE

Hylaeus sp.

HALICTIDAE

Dialictus sp.

Halictus farinosus?

Lasioglossum sp.

Sphecodes sp.

ICHNEUMONIDAE

MEGACHILIDAE

Osmia sp.

SPHECIDAE

HEMIPTERA

LYGAEIDAE

DIPTERA

ANTHOMYIIDAE

Scatophaga sp.

BOMBYLIIDAE

Bombylius sp.

Conophorus sp.

CONOPIDAE

Myopa sp.

DOLICHOPODIDAE

EMPIDIDAE

MUSCIDAE

Phormia sp.

RHAGIONIDAE

SEPSIDAE

Sepsis? sp.

SYRPHIDAE

STRATIOMYIDAE

TEPHRITIDAE

COLEOPTERA

CERAMBYCIDAE

COCCINELLIDAE

DASYTIDAE

DERMESTIDAE

MELYRIDAE

LEPIDOPTERA

INCURVARIIDAE

Adela sp.

NOCTUIDAE

Schinia sp.

Limnanthes

HYMNENOPTERA

ANDRENIDAE

Andrena (Diandrena) cuneilabris

Andrena (Euandrena) caerulea

**Andrena (Hesperandrena) limnanthis*

Andrena (Melandrena) sp.

Andrena (Plastandrena) prunorum

Andrena (Tylandrena) layiae

Andrena spp.

Calliopsis (=Nomadopsis) sp.

**Panurginus occidentalis (Crawford)*

SPECIALIST BEE POLLINATORS OF SHOWY VERNAL POOL FLOWERS

APPENDIX II (continued). Flower Visitor Guilds of Showy Vernal Pool Plant Taxa. * denotes oligolectic bee species.

<i>Panurginus</i> sp.	HEMIPTERA
ANTHOPHORIDAE	CICADELLIDAE
<i>Diadasia nigrifrons</i>	MIRIDAE
<i>Melissodes</i> sp.	LEPIDOPTERA
<i>Nomada</i> sp.	HESPERIIDAE
<i>Synhalonia</i> sp.	INCURVARIIDAE
<i>Xeromelecta</i> sp.	<i>Adela</i> sp.
APIDAE	LYCAENIDAE
<i>Apis mellifera</i>	NOCTUIDAE
<i>Bombus bifarius</i>	<i>Schinia</i> sp.
<i>B. californicus</i>	SATYRIDAE
<i>B. caliginosus</i>	
<i>B. edwardsii</i>	Downingia
<i>B. occidentalis</i>	HYMNENOPTERA
<i>B. sitkensis</i>	ANDRENIDAE
<i>B. vosnesenskii</i>	<i>*Panurginus atriceps</i>
CHRYSIDIDAE	ANTHOPHORIDAE
EUMENIDAE	<i>Nomada</i> spp.
HALICTIDAE	<i>Anthophora urbana</i>
<i>Agapostemon texana</i>	APIDAE
<i>Dialictus</i> sp.	<i>Apis mellifera</i>
<i>Halictus (Seladonia)</i> sp.	<i>Bombus huntii</i>
<i>Lasioglossum</i> sp.	<i>B. vosnesenskii</i>
ICHNEUMONIDAE	COLLETIDAE
MEGACHILIDAE	<i>Hylaeus</i> sp.
<i>Hoplitis</i> sp.	HALICTIDAE
<i>Osmia</i> sp.	<i>Dialictus</i> sp.
SPHECIDAE	<i>Evylaeus</i> sp.
DIPTERA	<i>Halictus (Seladonia)</i> sp.
ANTHOMYIIDAE	MEGACHILIDAE
<i>Scatophaga</i> sp.	<i>Osmia</i> spp.
BIBIONIDAE	POMPILIDAE
BOMBYLIIDAE	DIPTERA
CONOPIDAE	ANTHOMYIIDAE
<i>Physocephala</i> sp.	<i>Scatophaga</i> sp.
DOLICHOPODIDAE	MUSCIDAE
EMPIDIDAE	<i>Phormia</i> sp.
MUSCIDAE	SYRPHIDAE
<i>Phormia</i> sp.	COLEOPTERA
SEPSIDAE	CHRYSOMELIDAE
<i>Sepsis?</i> sp.	COCCINELLIDAE
SYRPHIDAE	DASYTIDAE
<i>Scaeva</i> sp.	MELOIDAE
<i>Eristalis</i> spp.	<i>Meloe</i> sp.
COLEOPTERA	LEPIDOPTERA
BUPRESTIDAE	INCURVARIIDAE
CANTHARIDAE	<i>Adela</i> sp.
CERAMBYCIDAE	SATYRIDAE
CHRYSOMELIDAE	HEMIPTERA
COCCINELLIDAE	MIRIDAE
DASYTIDAE	
ELATERIDAE	
PEDILIDAE	
SCARABAEIDAE	