

Biology of Specialist Bees and Conservation of Showy Vernal Pool Flowers. A Review.

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ABSTRACT. Some native solitary bees of the genera *Andrena* and *Panurginus* (family Andrenidae) and several showy vernal pool flowering plants have evolved close ecological relationships. Females of these bee species specialize on flowers of specific genera as sources of pollen to feed their brood. In turn, the female bees provide essential pollination services to their pollen flowers. These partners have annual life cycles with close synchrony between adult bee activity and flower bloom, both in space and time. Most of the bees nest in uplands outside the perimeter of the pools in which their pollen hosts grow. Pollination services provided by the bees link the pools to the surrounding uplands. Mitigations need to take into account the presence of pollinators and their habitats surrounding pools to maintain a viable long-lasting characteristic vernal pool flora.

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INTRODUCTION

This review summarizes research on the relationships of native bees and the ecological service, pollination, that bees provide to the characteristic showy plants of vernal pool ecosystems in California. There are many insect visitors to these flowers. Visitors vary in their relative efficiency to provide pollination services to flowers. The bee species of primary interest are those in which the females are oligoleges (*oligo*, few + *legere*, to gather), that is, bees that specialize in collecting pollen from one or a few closely related flowering plant species. Specialist female bees also tend to be the most numerous visitors to their host flowers. Experiments on *Blennosperma nanum* pollination (Leong, 1994) and observations on foraging behavior of most of the vernal pool oligolectic bees involving pollen removal and stigma contact (Thorp, 1990) suggest that oligolectic female bees are the most efficient pollinators of their host flowers.

RESULTS AND DISCUSSION

The Specialist Bees

Females of several native solitary ground nesting bee species in the family Andrenidae specialize in collecting pollen from flowering plants adapted to the prolonged inundation in vernal pools (Table 1). Females of each species of bee specialize on pollen of one genus of plants, especially on those plants

with mass floral displays. These showy, annual flowering plants, especially *Blennosperma*, *Downingia*, *Lasthenia* and *Limnanthes*, are often used to characterize the California vernal pool ecosystem. The oligolectic bees have annual life cycles in which adult bee activity is restricted to the few weeks in which their pollen host plants bloom.

Oligolecty. Specialization by pollen-foraging female bees in the vernal pool ecosystem is at the level of plant genera, especially the out-crossing species within these genera. Some of these plant genera contain species that are not restricted to vernal pool ecosystems. Oligoleges on *Lasthenia*, for example, are not restricted to only vernal pool species of goldfields, but also collect pollen from those species that live outside vernal pool ecosystems. These upland non-vernal pool flower species may help maintain metapopulations of vernal pool oligolectic bees when they occur in close proximity to vernal pool ecosystems.

Life cycle. Bees that specialize on vernal pool flowers have only a single generation per year. The adults are active above ground for only a few weeks each year. The majority of the life cycle is spent underground within brood cells with progeny undergoing feeding, growth, and eventually transformation from larvae to adults. The general life cycle for species of *Andrena* is illustrated and discussed by Thorp (1990) and Thorp and Leong (1995), and is available on the web at: www.vernalpools.org/Thorp/. Bio-

TABLE 1. Bee species (family Andrenidae) that specialize in collecting pollen from characteristic vernal pool flowers with showy displays.

Genus	Species	Pollen Host Genus
<i>Andrena</i>	<i>blennospermatis</i>	<i>Blennosperma</i>
<i>Andrena</i>	<i>puthua</i>	<i>Lasthenia</i>
<i>Andrena</i>	<i>submoesta</i>	<i>Lasthenia</i>
<i>Andrena</i>	<i>baeriae</i>	<i>Lasthenia</i>
<i>Andrena</i>	<i>duboisii</i>	<i>Lasthenia</i>
<i>Andrena</i>	<i>lativentris</i>	<i>Lasthenia</i>
<i>Andrena</i>	<i>leucomystax</i>	<i>Lasthenia</i>
<i>Andrena</i>	<i>pulverea</i> (= <i>limnanthis</i>)	<i>Limnanthes</i>
<i>Panurginus</i>	<i>occidentalis</i>	<i>Limnanthes</i>
<i>Panurginus</i>	undescribed (= <i>atricepes</i>)	<i>Downingia</i>

logical information including life cycles for species of *Panurginus* is discussed by Rozen (1967), Rust (1976), and Neff (2003). In the species of *Andrena* considered here, pupation occurs in autumn and the bees overwinter in their natal cells as adults prepared to emerge in early spring (Thorp, 1990). In contrast, species of *Panurginus* typically overwinter as post-defecating larvae (often referred to as prepupal larvae), pupate and emerge in late spring (Rozen, 1967; Neff, 2003).

Nest sites. Most specialist bees nest in uplands in the vicinity of their pollen host plants (Rust, 1976; Thorp, 1990). However, a few have been found nesting in the margins of pools and an undescribed species of *Panurginus*, that specializes on *Downingia* spp., may at times nest in the bottoms of the evaporated pools amongst its host plants (personal observation). Nests may be aggregated or solitary and scattered. Most are initiated in areas of bare soil or soil covered with sparse vegetation. Nests are often adjacent to or within patches of host plants, but in some cases they may be up to 100 meters away from host plants. Nests of the *Panurginus* specialist on *Downingia* are constructed in late spring as the soil begins to crack. Most often, they are initiated within soil cracks, making it difficult to locate their nest entrances.

Emergence. As is the case for many univoltine (single generation per year) solitary bees, the specialist bees in the vernal pool ecosystem are protandrous. That is, males emerge first and are available to mate with females as soon as they emerge a few days later. The males spend time cruising nest sites and flowers searching for mates. They stop occasionally to take up nectar from any suitable resource. Thus, their role in pollination of vernal pool flowers is similar to that of other generalist nectarivores. Fe-

males emerge, mate, forage initially for their own sustenance and then initiate nest construction.

Mating. Mating behavior and location is unknown for most of these bee species. Observations on mating in *Panurginus occidentalis* at flowers are described by Rust (1976). Males are frequently observed cruising preferred host plants of the female bees, presumably in search of females. Courtship approaches by males, especially toward females with loads of pollen in their pollen transport structures, are usually rejected. These females are already mated and have initiated nest construction and pollen provisioning for their offspring.

Dispersal. Many solitary ground-nesting bees construct nests in the vicinity of the nest from which they emerge. Some must disperse, but what proportion, how often, how far, and under what conditions is virtually unknown. Presumably, dispersal is most likely to occur shortly after mating, probably in response to a lack of suitable forage in the nearby vicinity and/or changes in the natal nest site substrate that make it less than favorable for re-nesting.

Nest construction. After mating, female bees excavate shallow burrows. Detailed architecture of nests of some vernal pool oligoleges are described by Thorp (1990) for *Andrena* and Rust (1976) for *Panurginus*. While these may be considered typical for their respective genera, nests of most vernal pool oligoleges remain undescribed.

Typically, nests of *Andrena* have a vertical shaft four to six inches deep and capped by a concentric tumulus of excavated soil. The tumulus is closed when the female is excavating, usually through the late afternoon and night. When the burrow is open, the female is usually out foraging for food. At the bottom of the vertical shaft, several two to three inch horizontal lateral tunnels branch out, each terminating in an urn-shaped brood cell that angles slightly below the horizontal. The brood cell is lined with waterproof material secreted by the female. At this stage the females initiate foraging for pollen from their preferred host plants. After a few loads of pollen are deposited, nectar is added and the provisions take on a spherical form. Finally, an egg is laid atop the larval food mass and the brood cell is capped with soil particles in a spiral arrangement. The inside of the cell cap is not lined. The tunnel to the completed brood cell becomes filled with soil as the female excavates the next lateral tunnel.

As for *Panurginus*, the nests described by Rust (1976) (as *P. atriceps*), descend in a somewhat winding manner to a depth of about four to five inches. Up to 10 horizontal brood cells are spirally arranged around this vertical shaft. Most brood cells are within an inch of the main tunnel. The lining of the brood cell, the spherical pollen provisions, the egg placed atop the provisions, and the unlined brood cell cap are as described above for *Andrena*.

Inundated nests. Nests of the *Panurginus* specialist of *Downingia* observed at the bottom of the pools containing their host plants are underwater for varying periods of time, from one to several months, while the pools are inundated during the wet phase in winter (unpublished data). How they survive these conditions has not been investigated. In *Panurginus*, the brood cell, except for the cap, is lined with a waxy waterproof material. The small size of *Panurginus* brood cells, and the heavy clay-loam soils in which they nest may also play a roll in preventing water from penetrating the brood chamber.

Very few other bees whose nests are inundated for three to six months have been studied. However, two species that nest in sandy, seasonally inundated soils have been researched (Roubik and Michener, 1980; Norden et al., 2003). *Perdita floridensis* is in the same subfamily as *Panurginus*, but its brood cells lack any waterproof lining (Norden et al., 2003). Post-feeding larvae of *P. floridensis* move out of their brood cells into the surrounding sand. Nest sites may become inundated for several months during which the prepupae become seasonally aquatic. *Epicharis zonata*, studied by Roubik and Michener (1980), is in a very distantly related family of bees. Its brood cells are almost completely lined internally with a waxy waterproof material, including most of the cell cap, except for a small central micropyle area. Their brood cells also have a double entrance plug, which may afford additional protection from water.

Synchrony with host plants. Emergence and flight period of specialist vernal pool bees is highly synchronized with the bloom phenology of their host plants. How they are able to accomplish this is not well understood. Conditions that stimulate germination of the annual flowering plants occur long before flowering. Can these also trigger future emergence of the bees? Thorp (1990) provides an example of an oligolectic vernal pool bee, *Andrena pulverea* (as *A. limnanthis*), that was able to hold over more than

one drought year (1976-1978) to emerge in synchrony with its host plant *Limnanthes douglasii* that had not bloomed during that period. It is well known that many annual plants can hold over unfavorable years in the form of seed banks. Some desert bees are known to exhibit prolonged diapause, usually as post-defecating, prepupal larvae up to as long as 10 years (Houston, 1991) and some bees are parsivoltine with part of the population holding over more than one year (Torchio and Tepedino, 1982). However, the ability of bees to hold over as adults in their natal cell, is unusual and merits further study.

The role of rainfall patterns is one likely explanation of such synchrony. Evidence for unseasonal rainfall as a stimulus for normally spring-blooming desert plants to bloom and their oligolectic bees to occur with them in autumn, disjunct from their normal spring season, has been reported by Hurd (1957) and LaBerge and Thorp (2005).

Foraging behavior. Once female bees have established their nests and are ready to start provisioning their brood cells, they become central-place foragers flying out from and returning to fixed nests. These bees tend toward small body sizes and thus have rather small foraging ranges (Gathmann and Tschamtkke, 2002). Vernal pool oligolectic bees tend to exhibit 1) site fidelity, returning to the same pools and areas within these pools as visited in previous foraging bouts, 2) limited inter-patch foraging and 3) near neighbor movements within flower patches (Thorp, 1990; Leong et al., 1995). Thus, bee-mediated pollen flow tends to be concentrated and very localized with only rare long distance movements. This in turn may have important consequences on how pools should be constructed and restored in mitigation projects (Elam, 1998). Using population genetic theory, Elam (1998) identifies considerations for restoration projects and raises a number of questions that go unanswered in most mitigation. Included are the potential effects of alterations of bee-mediated gene flow, and thereby, local adaptations and plant population fitness. Ramp et al. (2006) show how genetic markers compared between restored and natural populations of the bee pollinated, endangered *Lasthenia conjugens*, can be used for decisions on conservation and restoration.

Systematics. Oligolectic bees of the genus *Andrena* that are found in vernal pool ecosystems in California have been described and named (Thorp, 1969; Thorp and LaBerge, 2005). However, andrenid bees in the genus *Panurginus* have not been revised re-

cently. There are two *Panurginus* oligoleges known to specialize on vernal pool flowers. Fortunately, they are the most recognizable within the genus. One of these species, the one associated with *Downingia*, has not yet been described or named.

Other Flower Visitors

Specialist bees are not the only visitors to showy vernal pool flowering plants. There are generalist bees, flies, beetles, butterflies, true bugs and thrips that have been found visiting vernal pool flowers (Thorp and Leong, 1998; Leong and Bailey, 2000). The relative importance of these flower visitors in pollination and reproduction of vernal pool plants requires future study.

Pollination

Recently there has been considerable discussion of specialization and generalization in plant-pollinator interactions (Waser and Ollerton, 2006). The showy vernal pool flowers considered here (*Blennosperma*, *Lasthenia*, and *Limnanthes*) are generalist flowers that have both specialist and generalist flower visitors. Only *Downingia* has what may be considered a specialized flower, but it also is visited by specialist and generalist flower visitors.

Blennosperma. A single specialist bee, *Andrena blennospermatis*, occurs through most of the northern part of the range of yellow carpets (Thorp and Leong, 1998) and pollinates both *B. nanum* and *B. bakeri*. Experiments conducted by Leong (1994) demonstrate that seed set in potted arrays of plants were significantly reduced at sites where the specialist bee was absent. The importance of the interdependence of this bee and its host flowers is briefly discussed in Thorp (1997).

Lasthenia. Six oligolectic species of *Andrena* (Table 1) overlap and fill most ranges of the obligate out-crossing species of goldfields (Thorp and Leong, 1998). Although many other insects visit *Lasthenia*, these specialist bees are probably the most effective pollinators based on their synchrony, flower visiting behavior and abundance in populations of *Lasthenia*. Generalist bees and some of the other flower visitors certainly may contribute to pollination of goldfields populations. However, their presence and abundance varies from site to site and it is questionable whether they would be sufficient to maintain thriving populations in the absence of the specialist bees. This hypothesis is in need of testing.

Limnanthes. Two species of oligolectic bees, *Andrena pulverea* (as *A. limnanthis*) and *Panurginus occidentalis*, overlap in distribution and fill most of the ranges of the out-crossing species of meadow-foam (Thorp and Leong, 1998). These are probably the most effective *Limnanthes* pollinators, although there are many other visitors. Females of *Andrena pulverea* (as *A. limnanthis*) far outnumbered all other bees in pan-trap sampling study conducted by Leong and Thorp (1999). Generalist bees and some other visitors may contribute to pollination of the plants, but the occurrence and abundance of many may not be reliable enough to maintain healthy populations. Since female pollen foraging bees remove considerable pollen from these and other vernal pool flowers, there is a need to demonstrate the effectiveness of pollen deposition on stigmas. Commercial populations of *Limnanthes alba*, grown for oil seed production, rely on large populations of managed pollinators such as honey bees and the generalist solitary bee, *Osmia lignaria propinqua* (Jahns and Jolliff, 1990, 1991; Jahns et al., 1997).

Downingia. One oligolectic bee, an undescribed species of *Panurginus*, is known to occur through most of the north central part of the range of the out-crossing species of skyblues (Thorp and Leong, 1998). It is likely the most effective pollinator, based on visitation behavior of females in which "safe sites" on the upper surfaces of the thorax become loaded with pollen that is not groomed, but remains available for pollen transfer among flowers (Thorp, 1990). These bees also have specialized stiff seta-like hairs on the lower face for extraction of pollen for their own use (Thorp, 2000).

A matching large bee pollinator that would receive pollen nototribically from species of *Downingia* that have long anther tubes has not yet been found. However, Thorp (1990) has observed small sweat bees climbing sexual columns of these flowers and working them in a manner to release pollen on to them sternotribically. Subsequently, I have seen females of the specialist *Panurginus* work them in the same manner (personal observations).

With respect to generalist visitors of *Downingia*, Gray and Leong (2004) found that workers of *Bombus vosnesenskii* exhibited buzz pollination behavior at flowers of *D. bella*, and, that this was effective in releasing pollen onto their heads. However, they did not measure their effectiveness resulting in successful seed set. This bee is not commonly found at *Downingia* flowers, and is not a reliable pollinator.

Wood (1961) noted that *Downingia pusilla* appears to be self-pollinating, setting abundant seeds in culture in contrast to other species of *Downingia*. Schmidt (1980) remarks that *Downingia* rarely set seed when planted in gardens, indicating that generalist pollinators are usually not sufficient to pollinate the flowers of out-crossing species of the genus. The specialized mechanism for pollen release in flowers of *Downingia*, described in detail by Wood (1961) and its operation by specialized pollinators (Thorp, 1990, 2000), may limit seed production in gardens where specialist pollinators are not available.

Self-fertile plants. Plant species such as *Pogogyne abramsii* are self-fertile and set sufficient seed from visits by generalist pollinators to maintain populations even in created pools (Schiller et al., 2000). Thus, pollinator limitation may not be as problematic for populations as issues of plant population density or plant size, which suggests resource limitation (see also Black and Zedler, 1998).

There are also self-fertile populations of the four plant genera emphasized here, such as: *Blennosperma chilense* (Ornduff, 1964), *Lasthenia glaberima* (Ornduff, 1966), *Limnanthes floccosa* (Arroyo, 1974), and *Downingia pusilla* (Wood, 1961) that do not rely on any pollinators. However, some gene flow from occasional insect-mediated pollen may benefit their populations genetically.

Mitigation

Because vernal pool ecosystems are temporary wetlands, home to many endangered species, and under threat from development, measures to protect vernal pool ecosystems and mitigate for their loss are necessary. Preservation and management of intact viable vernal pool ecosystems is the best conservation option. Other mitigation may involve mitigation banks, on-site restoration of degraded habitats, or off-site creation of new pools in areas where none previously existed. Pools may be monitored for a limited time, usually a requisite five years, before accepted as successful by governmental agencies. Most monitoring is focused on listed species under the federal and state Endangered Species Acts. Since none of the pollinators and few of the characteristic, showy vernal pool plants are accorded such protection, usually they are not monitored. However, as I have demonstrated here and in earlier publications, the pollinators, particularly specialist bees, play an essential role in the maintenance and reproduction of

plant populations that characterize California vernal pools.

Off-site creation of vernal pools usually results in loss of specialist bee populations because nests are destroyed when the original upland habitats are developed. Increasing density of pools as replacement in mitigation banks is done at the expense of upland nesting habitat for bees. It also may alter bee-mediated gene flow patterns and change the genetic structure and local adaptations of plant populations.

Thus, preservation and conservation of healthy vernal pool ecosystems needs to consider the landscape surrounding the pools, not just the pools themselves. Pollinators spend much of their life cycle outside pools and contribute an important ecological service to the showy flowers that live within pools. Creation of new pools, increasing densities of pools in mitigation banks, and the restoration of degraded pools that do not consider these external services will not produce healthy, viable, long-lasting, vernal pool ecosystems.

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