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Abstract. Trap nests were used to assay species richness, abundance and distribution of cavity-nesting insects in California's Sierra Nevada foothills bordering the Sacramento Valley. Particular focus was placed on the agriculturally significant native bee *Osmia lignaria* Say, 1836 because of its potential use as a pollinator of local orchard crops. *Osmia lignaria* and four other species were obtained from half of the eight study sites. Unidentified nests were constructed at the remaining sites. The strength of correlation between three habitat variables and species abundance was determined. Floral resource availability yielded the strongest correlation, followed by habitat type, then proximity to water. These findings document the presence of cavity-nesting native bees and their associates, highlighting their potential in pollinating important agricultural crops.

Key Words. Pollination, trap nests, *Hoplitis*, *Trichodes*, conopid flies.

Introduction

Osmia bees (Megachilidae) comprise over 350 species ranging widely in the northern hemisphere (Ascher & Pickering 2011). The North American blue orchard bee, *Osmia lignaria* Say, 1836, has been recorded from 55°N latitude in Canada to 30°N in Mexico (Rust 1974). The nominate subspecies is found east of 100°W; those populations west of the 100th meridian are referred to as *O. lignaria propinqua* (Rust 1974). All populations occur between sea level and 2000 m (Bosch & Kemp 2002), though the effects of elevation on local distribution are poorly understood (Bosch & Kemp 2002, Barthell et al. 1997). Although *O. lignaria* is of particular interest because of its potential use as a crop pollinator (Torchio 1981, Vaughan et al. 2007), we have only limited understanding of its preferred habitats, nesting habits or natural enemies in the wild (Barthell et al. 1997).

As is true of some other megachilid bees, *O. lignaria* is typically univoltine and a gregarious cavity-nester (Barthell et al. 1997, Eickwort 1975). Developmental rate and emergence are almost exclusively temperature-mediated (Bosch and Kemp 2000, Kemp 2005). Adults emerge from mid-March to late April, depending on prevailing conditions (Torchio 1989). Following emergence and mating, females undertake nesting activities for about one month (Phillips & Klostermeyer 1978). In four well-studied European *Osmia* species, females forage 150 m–1000 m from nests for construction and provisioning materials, and display specific floral preferences (Gathmann & Tscharntke 2002). North American *O. lignaria* females nest in existing cavities such as those bored into logs by cerambycid beetle larvae. Each cavity may contain numerous cells, separated by mud partitions. One egg is laid in each cell and provisioned with enough pollen to sustain the developing larva into adulthood. Typical brood sizes average about ten, occupying 2–3 cavities (Torchio 1984).

The diversity and abundance of *Osmia* spp. vary widely in space and time (Barthell et al. 1997). For example, one five-year study at the University of California's Hastings Reservation in Monterey County recovered a total of 602 *Osmia* specimens, representing 23 different species, with *O. lignaria* the most abundant (Barthell et al. 1997). A similar study at Hastings from 1937–1947 had produced only half as many specimens; in this case, *O. lignaria* was one of the rarest (Linsdale 1947).

Because *Osmia* nests readily in artificial materials (Torchio 1989), most surveys on *Osmia* populations involve trap-nesting methods; moreover, trap-nesting can be a valuable tool in surveying entire communities of cavity-nesting insects, their natural enemies, and resource availability. Reliable inferences about species richness can be made based on proportions of occupied and empty nest cavities (Tscharntke et al. 1998). Species richness estimates obtained from trap-nesting are closely correlated with those from sweep-net methods, and can serve as a correlate of plant species richness, owing to the interdependence of bees and local flora (Tscharntke et al. 1998).

Here we identify specific geographic locations and preferred habitats of local populations of *O. lignaria* and associated cavity-nesting insects in California's Sierra Nevada foothills adjacent to the Sacramento Valley. We document the diversity, relative abundance, and nesting preferences of *O. lignaria* in light of its potential role as a commercial pollinator in this important agricultural region.

Methods

We established one elevational transect ranging from low to moderate altitudes, as well as three additional study areas at moderate elevations in Butte and Plumas Counties, California. A total of eight sites was established. Sites varied according to water source, distance to water from trap nests, elevation, floral resources and habitat type (as classified by dominant vegetation (Barbour & Major 1988)) (Table 1). Some water sources were permanent, e.g., rivers, streams or lakes; others, ephemeral, e.g., springs. We selected sites at which there was an abundance of flora; all floral resources were identified to at least genus level.

A total of 83 identical trap nests was used. Nests consisted of wooden blocks into which holes were drilled and cardboard straws inserted. Each block was 45 cm long, 9 cm wide and 14 cm deep. Holes were 7 mm in diameter and were drilled completely through the 14 cm axis. The rear of the blocks was sealed with duct tape lightly coated in sand to prevent the nesting bees from becoming entangled. Each block had a total of 88 evenly spaced holes, four down and twenty-two across; hence, the total number of holes for nesting was 7304. Blocks were placed 0.5–1.5 m above ground level, on fallen logs, boulders, or in crotches of tree branches. Trap nests were otherwise oriented randomly. Blocks were placed in selected sites from 20 Apr–30 Apr 2005 (the earliest possible dates given the limitations of the study), then retrieved from 22 Jun–14 Jul 2005.

Mud plugs or partitions in individual holes were considered evidence of nesting. Blocks were further inspected for signs of nesting activity by removing the tape from the back of the wood blocks and shining a flashlight into each hole. Those blocks showing no sign of nesting activity were removed from the experiment. The remaining trap nests were re-taped and stored indoors at temperatures ranging from 29°–34°C until 24 Aug 2005. Thereafter, nests were relocated to a second storage area, where temperatures ranged from 23°–26°C and the ambient relative humidity

Table 1. Description of study sites.

Location (County)	Latitude, longitude, elevation (m)	Habitat	Dominant pollen and nectar sources	Dominant vegetation	Water source and distance from trap nest (m)
Wilder Drive, Bottom (Butte)	N39°47.0′ W, 121°43.6′ (205)	Oak woodland	*Dichelostemma* sp., *Lupinus* spp., *Mimulus* spp., *Cercis occidentalis, Ceanothus* spp.	*Quercus douglasii, Q. lobata*	Stream (5)
Wilder Drive, Middle (Butte)	N39°47.1′ W, 121°43.4′ (230)	Oak woodland	*Lupinus* spp., *Dichelostemma* sp., *Mimulus* spp.	*Quercus douglasii, Q. lobata*	Springs (20) Stream (200)
Wilder Drive, Top (Butte)	N39°48.0′ W, 121°43.3′ (445)	Chaparral	*Ceanothus* spp., *Eschscholzia californica, Blennospermum nanum*	*Arctostaphylos* spp., *Ceanothus* spp.	Springs (500)
H-Line (Butte)	N40°30.0′ W, 121°23.3′ (915)	Sierran coniferous forest	*Cercis occidentalis, Ceanothus* spp., *Arctostaphylos* spp., *Lupinus* spp.	*Pinus jeffreyi, P. ponderosa*	Stream (1000)
Paradise Lake (Butte)	N39°75.6′ W, 121°60.4′ (775)	Sierran coniferous forest	*Cornus nutallii, Arctostaphylos* spp., *Dicentra formosa, Vinca minor*	*Pinus jeffreyi, P. ponderosa*	Lake (250)
Belden Rest Area (Plumas)	N40°0.5′ W, 121°15.1′ (700)	Chaparral	*Eschscholzia californica, Lupinus* spp., *Brassica* sp.	*Arctostaphylos* spp., *Toxicodendron diversilobum*	River (25)
Belden Town* (Plumas)	N40°1.0′ W, 121°13.7′ (700)	Chaparral	*Eschscholzia californica, Lupinus* spp., *Lathyrus* sp.	*Arctostaphylos* spp., *Ceanothus* spp., *Pinus jeffreyi, P. ponderosa*	River (10)

* Although the Belden Town site borders chaparral and Sierran coniferous forest, we classified it as chaparral on the assumption of greater resource availability for nesting *Osmia* bees.

Table 2. Nesting activity of *Osmia lignaria* and associated cavity-nesting insects among study sites.

Location	Nests constructed	Nests occupied	Nests w/ *O. lignaria*	Other species present
Wilder, Bottom	48	7	2	*Hoplitis albifrons* *Euodynerus* sp. *Physocephala* sp.
Wilder, Middle	11	6	4	None
Wilder, Top	19	0	0	None
H-Line	6	0	0	None
Overlook	24	0	0	None
Paradise Lake	12	0	0	None
Belden Rest Area	30	5	0	*H. albifrons* *Euodynerus* sp.
Belden Town	5	3	1	*Euodynerus* sp. *Trichodes ornatus*

from 37%–44%. Nests remained under these conditions until 14 Sep 2005 and were subsequently maintained at 4°C until 13 Feb 2006, after which nests were continuously incubated at approximately 22°C.

Emergence capsules were attached individually to the outside of all holes showing signs of nesting activity. Capsules consisted of 1 dram glass vials; short straws were wedged partially into the neck of each vial and attached to the trap nests by inserting the protruding end of each straw into the nest holes. The adult bees were thus forced to emerge through the straws and directly into the vials. Nests were checked daily and any signs of emergence recorded. Nests were left otherwise undisturbed from 13 Feb–15 Mar 2006, after which the duct tape was removed from the back end of the blocks, and nest contents were extruded from individual holes and into the attached vials. All intact specimens and nest contents were retained for reference.

Specimens were identified using published keys (Rust 1974, Foster 1976) and identifications verified by Dr. R. Thorp (Department of Entomology, University of California, Davis). Voucher specimens were deposited in the California State University, Chico Entomology Collection. We performed correlation analyses to estimate the strength of association between the number of nests constructed and proximity to floral resources and water. We calculated correlation coefficients between nesting blocks, habitat type and site elevation. Statistical analyses were performed with JMP IN® 5.1.2 (SAS Institute 2004).

Results

Fifty-four nest blocks were recovered; in 20 of these, 155 nest holes showed evidence of nesting activity (Table 2). Visible signs of nesting activities ranged from complete nest plugs, to partial end plugs, to holes lacking plugs but showing evidence of internal cells. Successful emergence or recovery of specimens occurred in 21 of the 155 occupied nest holes. We recovered no specimens from the remaining 134 holes, despite apparent nesting activities. Most of the plugs appeared to be constructed purely from mud, consistent with published descriptions of nesting materials for *O. lignaria* (Bosch & Kemp 2002, Cane et al. 2007); however, some had masticated leaf material mixed in as well.

Despite the low rate of recovery, we identified 39 specimens representing six taxa of cavity-dwelling insects from four of our study sites (Table 2). Taxa included *O. lignaria* (two subspecies), *Hoplitis albifrons* Kirby, 1837 (Hymenoptera: Megachilidae), *Euodynerus nr. foraminatus* Saussure, 1853 (Hymenoptera: Vespidae) and two natural enemies: a predatory beetle, *Trichodes ornatus* Say, 1823 (Coleoptera: Cleridae), and a parasitic fly, *Physocephala* sp. (Diptera: Conopidae). Twenty-two insects emerged during incubation between 13 Feb–15 Mar 2006, including 13 *O. lignaria* and nine *Euodynerus* sp. We verified that developing bees had indeed reached maturity by removing and identifying one live adult *O. lignaria* prior to overwintering. The remaining 16 specimens were obtained by extraction of nest contents between 15 Mar–3 Apr 2006; these included one dead adult and one dead pupa of *O. lignaria*. From the abdomen of this pupa protruded the puparial fragment of what was evidently a conopid fly, *Physocephala* sp. Six dead *Euodynerus* sp. were also found during nest extraction. A total of seven specimens were recovered live during nest extraction, including five *H. albifrons*, one *Euodynerus* sp., and one *T. ornatus*. Four additional, partial specimens were recovered that could not be clearly identified: these are not included in our data set. However, based on their size, shape and color, as well as distinctive fecal pellets, cocoon construction and nest plugs, they appeared to be *O. lignaria.* A fifth incomplete specimen was extracted, apparently an additional dead *Euodynerus* specimen.

Thirteen of the 15 adult *O. lignaria* recovered were identified as the western subspecies *O. lignaria propinqua*; two were tentatively identified as the eastern subspecies *O. lignaria lignaria* (R. Thorp, personal communication). One putative *O. l. lignaria* was recovered from the Wilder, Bottom site; the other, from the Belden Town site. One nest cavity housed seven individual *O. l. propinqua*, while none of the remaining cavities yielded more than two specimens. Estimated occupancy rates of *O. lignaria,* based on total number of nests constructed, ranged from 0.29%–1.93%.

Nest number per site was positively correlated with proximity to water, but negatively with elevation (explaining 16% of the variance in among-site nest number). Using pair-wise confidence intervals (CI = 95%), the correlation coefficient between the number of nests constructed and the presence of chaparral was an estimated 0.273–0.423, while the correlation coefficient between nests constructed and the presence of oak woodland was 0.304–0.457. Because some California *Osmia* populations are strongly associated with *Lupinus nanus* Benth. (Fabaceae) (Knops & Barthell 1996), we noted in particular its presence at our study sites. The correlation coefficient between number of nests constructed and the presence of *Lupinus* spp.was estimated as 0.737–0.863.

Although 24 nests were constructed at Overlook, the highest site surveyed (Table 1), all were empty. The plugs were of pure mud, thus may have been made by *O. lignaria, Euodynerus* sp., or another, unidentified higher elevation species. No nests were found below 200 m (Table 2), but, given the limited elevational range surveyed in this study, *O. lignaria* appears most abundant in foothill habitats between 200 m–700 m. Our data suggest the cavity-nesting insects discussed here preferred chaparral or oak woodland habitat to coniferous forests, which may reflect the availability of necessary resources such as nesting sites, pollen sources and water.

Discussion

This study documents the occurrence, distribution and habitat characteristics of wild populations of *O. lignaria*, as well as associated cavity-nesting insects, in the Sierra Nevada foothills adjacent to the Sacramento Valley agricultural region. The population density of solitary bees such as *O. lignaria* in a given area is often lower than that of many other insects (Jayasingh & Freeman 1980). Thus our data, although suggesting low levels of abundance, are significant in identifying suitable habitats for cavity-nesting bees with similar habitat requirements as *O. lignaria* (Jayasingh & Freeman 1980, Tscharntke et al. 1998). Because the peak nesting season may have occurred prior to trap-nest placement, the densities of *O. lignaria* reported here are likely underestimates. Since female fecundity declines with advancing age, the lateness of the study season could further explain the apparently low density of bees found per cavity (Torchio 1989).

The presence of the eastern *O. lignaria lignaria* is noteworthy. Both subspecies of *O. lignaria* are very similar in morphology (R. Thorp, personal communication). In female bees at least, *Osmia l. propinqua* is distinguished by the presence of four mandibular teeth; *O. l. lignaria* has but three mandibular 3 teeth, the first and second fused to form a ridge (Rust 1974). Two specimens collected in our study were tentatively identified as *O. l. lignaria* (R. Thorp, personal communication), well outside the established range of *O. l. lignaria* (Rust 1974). Numerous trials have been conducted in Sacramento Valley orchards using *O. lignaria*, and it is routinely purchased for agricultural use across North America without regard to subspecies; thus, *O. l. lignaria* may have been inadvertently released outside its normal range.

Many cavity-nesting solitary native bees have shared habitat and floral resource requirements (Chaplin-Kramer et al. 2011). For example, although most native bee species are generalists, some possess physical attributes (i.e., body size and tongue length) optimally suited for foraging on a particular suite of plants (Black et al. 2011). Thus, there are often associations between specific floral resources and the bee species foraging on them (Neal Williams, personal communication). Further, most native bees have specific nesting preferences, and can be classified as either ground- or tunnel-nesters. Tunnel-nesters typically require a source of water, mud or vegetation for nest construction (Mader et al. 2011). The two megachilids found in this survey, *H. albifrons and O. lignaria,* have similar flight periods, require similar nesting materials, and were trap-nested in the same two sites, suggesting they indeed prefer similar habitats. In this sense, these two bee species could be considered associates.

In northern California, many cavity-nesting *Euodynerus* occur, although keying these to species level is often problematic (L. Kimsey, personal communication). Like *Osmia,* the *Euodynerus* collected in this study (probably *Euodynerus foraminatus*) nests in pre-existing wood cavities, using mud to construct nest plugs and cells (Evans & West-Eberhard 1970). While they do not share as many specific habitat preferences with *O. lignaria* as do *H. albifrons,* the close similarity in nesting substrates suggests these species are ecological associates as well.

Conclusion

Although the honey bee (*Apis mellifera* Linnaeus, 1758) has been relied upon as the major pollinator of many orchard crops, the honey bee industry has declined recently owing to habitat loss, increased pesticide use, and parasitic mite outbreaks

(Allen-Wardell et al. 1998, Kremen et al. 2002). *Osmia lignaria* has shown great promise as a pollinator of commercial orchards, as it will nest in artificial materials, can be easily managed for pollination purposes, and has demonstrated a floral preference for many orchard crops (Torchio 1981). Documenting and encouraging sufficiently abundant local populations of *O. lignaria* and associated native pollinators, and preserving the habitats in which they are found, can aid commercial pollination efforts in the Sacramento Valley and other agricultural regions. In the interest of gaining a more accurate understanding of nesting ecology of *Osmia* and other solitary bees, it will prove critical to initiate further trap-nesting studies well in advance of the anticipated flight season.

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