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The Phenology and Spatial Distribution of Cavity-Nesting Hymenoptera and Their Parasitoids in a California Oak-Chaparral Landscape Mosaic

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ABSTRACT.—Spatial resource distribution and phenology are critical factors for the development, emergence, and reproduction of solitary hymenopterans. However, the biotic and abiotic conditions that drive changes in their spatiotemporal distributions remain poorly understood. We surveyed the cavity-nesting hymenopteran community in a region of California oak-chaparral habitat over 3 y. Most taxa had short seasonal activity periods, with >90% of observations occurring within a single month for six of eight taxa studied. Predaceous wasps including *Euodynerus foraminatus* and *Trypoxylon tridentatum* were most abundant during the warmer mid-season months, while megachilid bees showed divergent phenologies consistent with temporal niche separation by species. Similarly, while some taxa were abundant and widespread across the study site, most showed relatively restricted spatial distributions. Spatial distributions were only partially explained by the dominant vegetation type; although some taxa showed significant preferences for oak- or chamise-dominated habitats, in most cases, differences in nesting abundance were not statistically significant. Parasitism rates ranged from zero to 57% among reared host taxa, with the relatively generalist *Monodontomerus* spp. as the most common parasitoids observed. These observations describe a community with strong within-population phenological synchrony, variation in species distribution patterns, and species composition influenced by spatial habitat heterogeneity.

INTRODUCTION

Cavity-nesting bees and wasps are critical members of many terrestrial communities. This diverse group of hymenopterans includes several ecological guilds (pollinators, predators, and parasitoids) and often comprises insect communities with high species richness and trophic diversity (Ebeling *et al.*, 2012). Although these species are widespread within the natural world, much of our knowledge of their ecology comes from studies performed in agricultural and other human-managed landscapes (*e.g.*, Steffan-Dewenter and Leschke, 2003; Jenkins and Matthews, 2004; Loyola and Martins, 2006; Holzschuh *et al.*, 2009). In comparison, few have investigated the biotic and abiotic conditions that drive changes in abundance and spatial distribution within natural landscape mosaics (*but see* Sobek *et al.*, 2009).

Seasonal phenology plays a vital role in the development and emergence of cavity-nesting hymenopteran species (Kemp and Bosch, 2005). Each season, these species have a limited window of time in which to successfully emerge and reproduce. Solitary bees are dependent on ephemeral floral resources, whereas wasps generally collect prey of a specific species, size, or instar (Fig. 1; Krombein, 1967). These foraging constraints may have substantial effects on the behavior of individual species. In the Sonoran and Mojave deserts, for instance, specialist cavity-nesting bee species emerge synchronously with the bloom of creosote bush (*Larrea tridentata*) and facultatively enter diapause in the years that *L. tridentata* does not flower (Minckley *et al.*, 2000). The parasitoids of solitary bees and wasps must also time their

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FIG. 1.—Cross section of a nest provisioned by a eumenine wasp. Mud walls create distinct partitions between brood cells containing caterpillar prey. Photo credit: L. H. Yang

oviposition within an often narrow window of host suitability. Chrysidid parasitoids, for instance, have a short period of time in which to locate and oviposit in completed nests of mud-dauber wasps (Hymenoptera: Sphecidae) before the mud hardens (O'Neill, 2001). Parasitoids in the genus *Monodontomerus* (Hymenoptera: Torymidae) must oviposit in the cocoon of a late instar bee or wasp larva in order to develop to maturity (Eves, 1970). Parasitizing an early instar bee larva invariably results in the death of the host and the parasitoid, creating strong stabilizing selection to time parasitoid oviposition with host development (Eves, 1970).

Because suitable abiotic conditions and resources are often distributed patchily throughout the landscape, solitary bees and wasps generally have discrete spatial distributions concentrated in habitat types that align with their resource needs (Potts *et al.*, 2005). A study comparing solitary bee and wasp colonization in crop and fallow fields in Germany reported significantly higher bee species richness and nesting in fields with high floral diversity than fields with low floral diversity (Gathmann *et al.*, 1994). These results suggest solitary bees select nest locations near areas with higher quality and more abundant floral resources. Similarly, long-term sampling efforts in Costa Rica have revealed two closely-related ground-nesting solitary bee species in the genus *Centris* (Hymenoptera: Anthophoridae) co-occur in coastal areas but appear to segregate their nest locations based on vegetation types (Frankie *et al.*, 1993). A number of other factors may drive these species-specific differences in spatial distribution, including temperature sensitivity of larval stages, availability of preferred nest sites, and parasite pressure (Vinson *et al.*, 1987; Vinson and Frankie, 1988; Frankie *et al.*, 1993). Because resource availability fluctuates in response to changing environmental conditions, it is also likely that nest location preferences of cavity-nesting bees and wasps shift over time.

Despite interspecific differences in nest location preference, solitary hymenopterans across a broad taxonomic range display aggregative nesting behavior (Michener *et al.*, 1958; Rosenheim, 1990; Bosch, 1994). One proposed hypothesis for this behavior posits these nesting clusters provide increased protection from brood parasites and parasitoids (Wcislo, 1984). For instance, hosts that nest near conspecifics may benefit from improved group vigilance, group defense strategies, and/or parasite swamping (Rosenheim, 1990). For instance, some solitary hymenopterans have been observed aggressively defending their nests from parasites (Thorp, 1969; Torchio, 1989). However, of the limited number of studies that have documented parasitism rates in solitary hymenopteran nesting aggregations, most have focused on ground-nesting species (Larsson, 1985; Wcislo, 1986; Rosenheim, 1987; Antonini *et al.*, 2003), reporting both density-dependent and inversely

density-dependent correlations between parasitism rate and host population size. Currently, little is known regarding the relationship between host density and parasitism in solitary cavity-nesting bees and wasps. One of the few studies to examine this issue reported relationships between host density and the incidence of parasitism that varied from positive to negative density-dependence across years (Steffan-Dewenter and Schiele, 2008).

Although cavity-nesting bees and wasps generally nest in beetle burrows and hollow twigs (Krombein, 1967; Polidori *et al.*, 2011; Kraemer *et al.*, 2014), they will also accept artificial nest habitat in the form of paper nesting tubes and wooden nest blocks. Augmenting aboveground nest habitat (“trapnesting”) is a widely used survey method that can provide a wealth of information on cavity-nesting species, including species diversity, abundance, phenology, associated habitat, prey usage, parasitism, and nest architecture (Jenkins and Matthews, 2004). In this study we used this survey technique over 3 y in order to answer the following questions: (1) What is the seasonal phenology of a cavity-nesting hymenopteran community in its native habitat? (2) How are taxa spatially distributed among major habitat types? and (3) Does the density of cavity-nesting bees and wasps affect rates of parasitism? The objective of this study was to provide a temporally and spatially explicit description of the cavity-nesting hymenopteran community at one field site over multiple years.

METHODS

NATURAL HISTORY

Cavity-nesting bees and wasps construct linear nests, each consisting of several chambers. In the case of nonparasitic species, individual nest chambers contain a single egg and a food provision to sustain the developing larva. Female bees provision their nests with a nectar-pollen mixture, whereas solitary wasps may collect a variety of prey to provision their nests, including spiders (Araneae) or caterpillars (Lepidoptera) (Krombein, 1967). Once the female has inserted the food provision and egg into a cell, she gathers material (often mud or masticated leaf, depending on the species) to construct a partition before beginning the next cell. These partitions create distinct brood chambers for each developing larva. After the female has completed a series of cells, she seals the nest with a thicker mud or leaf plug. Most of the bees collected in this study were megachilids, including *Osmia lignaria*, a native bee that builds nest partitions from macerated mud (Bosch, 1994); *Anthidium maculosum*, a small native bee that lines its nest cells with plant trichomes (Alcock *et al.*, 1977); *Megachile apicalis*, an introduced European species that builds cell partitions with fragments of leaves or flowers (Barthell *et al.*, 2002); and *Hoplitis albifrons maura*, a native bee that builds partitions using macerated leaves and coarse mud (Michener, 1947). Among the common predaceous hymenopteran taxa observed in this study were *Trypoxylon tridentatum* (Crabronidae), a spider-provisioning specialist (Coville, 1986); *Isodontia elegans* (Sphecidae), a species that provisions with paralyzed Orthoptera (O’Neill and O’Neill, 2007); and two species of eumenines, *Euodynerus foraminatus* (Stahlhut and Cowan, 2004) and *Parancistrocerus mcclayi*. Throughout this study, a large number of eumenine wasps were collected as immatures, which could not be identified below the subfamily level based on larval morphology; these eumenines are conservatively identified only at the subfamily level throughout this manuscript. However, out of 81 larval eumenines reared from the 2011 season, 78 (96%) were *Euodynerus foraminatus*, and three (4%) were *Parancistrocerus mcclayi*. These identifications suggest that the majority of eumenines from this site are likely to have been *E. foraminatus*.

A number of parasitoids and cleptoparasites lay their eggs inside the nests of trapnesting bees and wasps. The common parasitoid taxon in our study region is *Monodontomerus torchioi* (Torymidae), while the most common cleptoparasitic species are in the family Chrysididae (*Chrysis nitidula*, *Chrysis apontis*, *Crysis inaequidens*, *Chrysura kyrae*, and *Caenochrysis deversor*). The key distinguishing factor between parasitoids and cleptoparasites is the consumption of host resources. Parasitoids in the genus *Monodontomerus* insert their ovipositor through the host cocoon and deposit 10-20 eggs on the developing host prepupa (Eves, 1970; Grissell, 2007). The parasitoid larva then consumes the host prepupa and develops inside the host nest. In contrast cleptoparasitic chrysidid wasps enter the host nest while the female is foraging and oviposit directly on the nectar-pollen provision. As it develops, the immature cleptoparasite consumes the nectar-pollen provision and often the developing host larva (Godfray, 1994).

STUDY REGION

The University of California Quail Ridge Natural Reserve (38°28'58.90"N, 122° 8'58.11"W) is located on a peninsula near the Berryessa Reservoir (Napa County, CA) and consists of over 1000 ha of land in the northern Coast Range. The reserve is a mosaic of chamise chaparral, oak woodland, and grasslands. Dominant plant species at the reserve include interior live oak (*Quercus wislizeni*), blue oak (*Quercus douglasii*), chamise (*Adenostoma fasciculatum*), toyon (*Heteromeles arbutifolia*), and mountain mahogany (*Cercocarpus betuloides*).

SAMPLE COLLECTION

In February 2010 we installed 36 approximately 1.5 m tall fence posts along dirt roadways within Quail Ridge Natural Reserve at 200 m intervals. Each post held 30 cardboard nesting tubes, mounted on the northeast side of the post with the nest openings facing southeast. We conducted our survey for three consecutive years (2010-2012), using different methods each year to capture different aspects of the community. Over the course of the study, two nest designs were used. In 2010 and 2011, we secured a composite board to the outside of each fence post, upon which 30 cardboard nesting tubes of three sizes (10 of each size: 4.76 mm internal diameter, 0.51 mm wall thickness; 6.35 mm internal diameter, 0.76 mm wall thickness; and 7.94 mm internal diameter, 1.02 mm wall thickness) were attached. Some solitary hymenopterans display preferences for nest cavities based on cavity diameter (Torchio and Tepedino, 1980; Fricke, 1991). Therefore, we included three nest tube sizes to provide nesting materials for both large and small-bodied species. The composite board design exposed nesting tubes to abiotic and biotic conditions similar to that of natural twig nesting habitat. In 2012 each fence post contained a 25 cm length of plastic PVC piping (15 cm inner diameter) designed to hold a bundle of 19 cardboard nesting tubes (7.94 mm internal diameter, 1.02 mm wall thickness). PVC pipe nests limited exposure to rainfall in a manner that was intended to mimic beetle burrows and other natural nesting sites. Lastly, we installed an iButton temperature logger (Maxim Integrated Products, San Jose, CA) on the northeastern aspect of each post in 2010 and 2011. Temperature loggers were adjacent to and covered by the cardboard tubes in order to collect microsite hourly temperature measurements.

SEASONAL PHENOLOGY STUDY

In 2010 we deployed 30 nest tubes at each post once a month, beginning on February 28, 2010 and ending on September 25, 2010. Each month, we collected the nest tubes from each

post and replaced them with empty nest tubes. We placed nesting tubes in individual bags and froze them to preserve all occupants. We then dissected nesting tubes and recorded the abundance of individuals within the tubes, as well as the type of provisions within each individual cell. By assessing the type of provision found within the cell (*e.g.*, pollen, spiders) and the mud wall architecture, we were able to identify many of the larvae within these nests to subfamily. Using these samples, we created a reference collection for Hymenoptera collected at the reserve.

OVERWINTERING COMMUNITY STUDY

In 2011 we deployed nest tubes on March 22, 2011 and collected them on February 11, 2012. In contrast to the 2010 survey, we collected all nests once at the end of the season in order to survey and rear the overwintering community, rather than performing monthly collections to survey the phenology of the spring-summer-fall community. Additionally, we dissected the nest tubes immediately following collection, rather than freezing them, in order to rear a subset to adulthood. This dissection and rearing of immature stages allowed us to build a more highly resolved reference collection for future identifications of immature stages. Upon dissection, we removed a representative sample of at least two living larvae and placed each larva into an individual gelatin capsule. We then reared individuals within the capsules at room temperature until the occupant either died or emerged from the capsule. We preserved additional larvae and all adults in alcohol. We identified all specimens to family and several to genus or species. Parasites that emerged from the reared specimens were identified, and overall parasitism rate was calculated as the total number of parasitized cells/the total number of host cells reared for each host taxon.

Similarly, for the 2012 survey, we deployed nest tubes on March 3, 2012 and collected them once on February 10, 2013. We identified the majority of nest occupants to family based on nest architecture, pupal case morphology, and provision type. We then recorded abundance and preserved all individuals in alcohol.

SPATIAL MAPPING

To assess the vegetation type at each of the nest posts, we used a publicly available vegetation map of Quail Ridge Natural Reserve (Thorne *et al.*, 2004). Because many of the previously recorded vegetation types on the map showed only slight differences (*e.g.*, “interior live oak” vs. “interior live oak/blue oak”), we consolidated all vegetation types into two main habitat classifications: chamise-dominated and oak-dominated. We then overlaid a map of the GPS coordinates from the 36 nest post locations over the vegetation map and recorded the primary surrounding vegetation type for each post (*i.e.*, the vegetation type covering the greatest land area).

STATISTICAL ANALYSES

Patterns in the temporal distribution (*i.e.* differences in abundances across months within a season) and spatial distribution (*i.e.*, differences in abundances between oak and chamise habitats) of each taxon were examined using permutational ANOVA (R Core Team 2015, lmpkg). In 2010 vegetation type and month were included as explanatory factors to predict the abundance per post for select taxa of interest. In 2011 and 2012, models included vegetation type as the only predictor, since these specimens were collected only once at the end of the season. A permutational approach uses 9,999,999 random iterations of the data to arrive at a stable test of significance that is not sensitive to underlying data

distributions. It has several advantages for this analysis and was selected after several alternative approaches were considered and rejected. Specifically, we considered using categorical analysis of the observed abundances compared with null expected abundances proportional to habitat availability using two-tailed exact binomial goodness-of-fit tests for comparing oak and chamise habitats (R Core Team 2015) and a Monte Carlo multinomial goodness-of-fit test to compare among months (R Core Team 2015, XNomial pkg). However, these analyses assume that each provisioned cell reflects an independent habitat choice, which is likely to be inaccurate and anti-conservative given that a single individual often provisions multiple cells. We also evaluated taxon-specific generalized linear models assuming underlying Poisson or negative binomial data distributions (with and without corrections for zero-inflation, Zeileis *et al.*, 2008) to evaluate the effect of vegetation type on the monthly abundances at each post. While competing models were evaluated based on standard goodness-of-fit criteria and the Akaike Information Criterion, model selection remained ambiguous and qualitative model results were sensitive to deviations from model assumptions. While computationally intensive, permutational ANOVA allowed for a single robust analysis without distributional assumptions.

We examined the relationship between eumenine abundance and nest parasitism using a generalized linear model (GLM) with a binomial error distribution and a logit link function (lme4, R Statistical Environment 2016) in order to test alternative hypotheses about the relationship between parasitism rate and host density.

RESULTS

TEMPORAL DISTRIBUTION

Monthly nest array collections in 2010 allowed us to investigate the phenology of taxa across the season. The majority of taxa collected had highly restricted temporal ranges. Six of eight surveyed taxa showed greater than 90% of observations in a single month, and the remaining two groups (Eumeninae and *Trypoxylon tridentatum*) had greater than 50% of observations occurring in a single month (Fig. 2). Most species for which more than 10 individuals were collected in 2010 showed a significant effect of month on abundance by post (permutational ANOVA; *Anthidium maculosum*, $P = 0.2245$, Apoidea, $P = 0.0002$, Eumeninae, $P < 0.00001$, *Euodynerus foraminatus*, $P = 0.0036$; *Megachile apicalis*, $P = 0.019$; *Osmia lignaria*, $P < 0.00001$; *Trypoxylon tridentatum*, $P = 0.091$). For several taxa larval development occurred primarily in July and August (Fig. 2), the period of the year with the highest daily mean and maximum temperatures in this region. However, among the megachilid bees, *Osmia lignaria* was a notably early-season species, *Anthidium maculosum* was most abundant in the mid-season, and *Megachile apicalis* was a distinctly late-season species (Fig. 2). The observed temporal distribution of *Euodynerus foraminatus*, *Parancistrocerus mcclayi*, and the unidentified Eumeninae is consistent with the identification of eumenine larvae as 96% *Euodynerus foraminatus* and 4% *Parancistrocerus mcclayi* in 2011 (Fig. 2). Both of these taxa bookend the peak of the eumenine larval phenology, suggesting provisioning adults were occasionally collected prior to the larval peak.

SPATIAL DISTRIBUTION

In 2010, 92 *Osmia lignaria* and 19 *Megachile apicalis* bees were collected from 17 and three nest posts respectively, with all collections for both species coming from oak-dominated habitats (Fig. 3). This observed difference in abundance between oak and chamise habitats reflected a significant preference for oak-associated habitats in *Osmia lignaria* (permutational

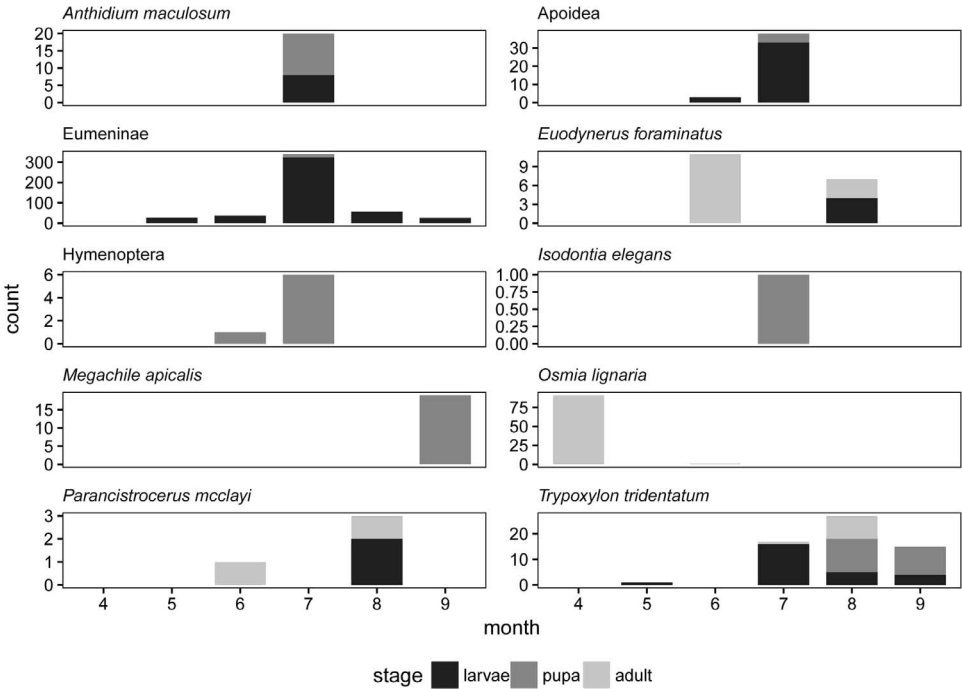


FIG. 2.—Temporal distribution of cavity-nesting taxa collected in 2010, separated by developmental stage. Larval development for most taxa occurred in July and August

ANOVA, $P = 0.041$), but this difference was not significant in *Megachile apicalis* (permutational ANOVA, $P = 0.273$). Similarly, 20 *Anthidium maculosum* bees were collected from a single post in chamise-dominated habitat; however, given the sparseness of these data, the effect of vegetation type was not significant (permutational ANOVA, $P = 0.224$). Among the predaceous hymenoptera, 492 eumenine wasps (probably dominated by *Euodynerus foraminatus*, see *Natural history*) were collected at 34 nest posts across all monthly collections. Eumenines were the most abundant and widespread hymenopteran taxon at the reserve (Fig. 3). The abundance of these wasps did not differ significantly in oak and chamise habitats (permutational ANOVA, $P = 0.934$). Similarly, 60 *Trypoxylon tridentatum* wasps were collected from 13 nest posts but were not significantly more abundant in oak habitats compared to chamise habitats (permutational ANOVA, $P = 0.281$, Fig. 3).

In 2011, 232 eumenines were collected from 24 nest posts (Fig. 4) using the same trapnest design, but a single collection protocol. The abundance of eumenines did not differ significantly based on habitat type (permutational ANOVA, $P = 0.4683$). Similarly, 71 *Trypoxylon tridentatum* were collected at 12 nest posts in 2011, but their abundance did not vary significantly by habitat type (permutational ANOVA, $P = 0.551$). Other taxa, including *Hoplitis albifrons maura* and *Isodontia elegans* were less common, with 43 *Hoplitis albifrons maura* and 17 *Isodontia elegans* collected at five nest posts and three nest posts, respectively (Fig. 4). Analyses of habitat preference for *Hoplitis albifrons maura* suggested a marginally significant preference for chamise habitats compared to oak habitats (permutational ANOVA, $P = 0.0574$). *Isodontia elegans* was only collected from oak habitats in 2011 but because of the high

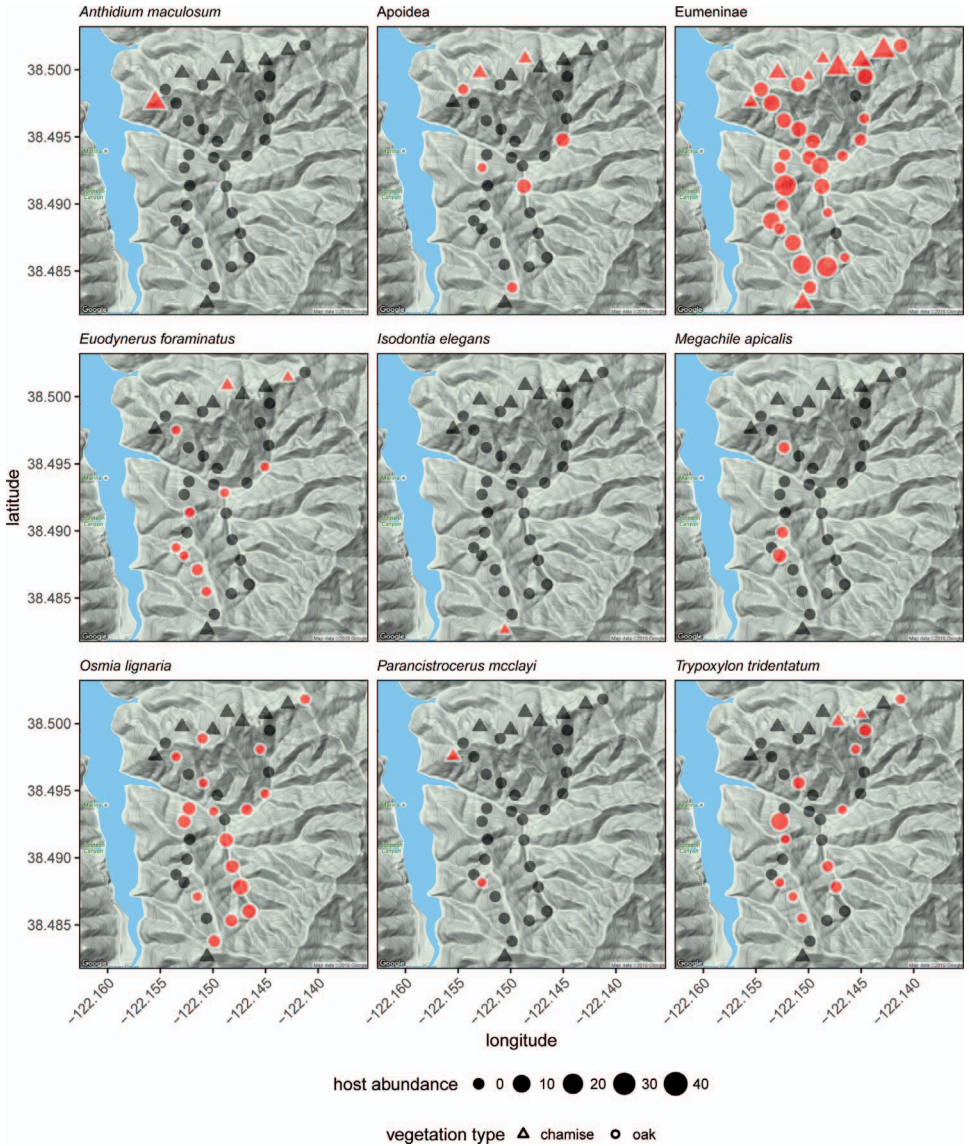


FIG. 3.—Spatial distribution of cavity-nesting taxa collected in 2010. Each point represents the location of a nest post containing 30 nesting tubes. Black points (without white outlines) mark locations where the focal taxon was not collected; red points (with white outlines) indicate locations where the focal taxon was collected. Post locations in chamise-dominated habitat are shown with triangles and those in oak-dominated habitat are shown as circles. Point size corresponds to host abundance. Full color version available electronically.

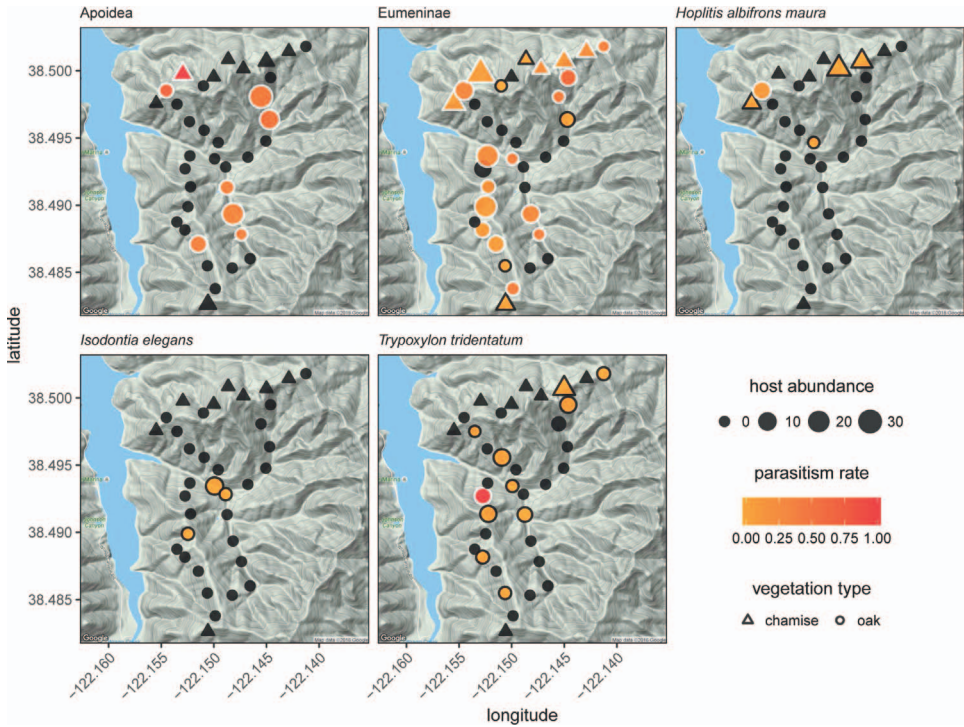


FIG. 4.—Spatial distribution of cavity-nesting taxa collected in 2011 and associated rates of parasitism. Points with a white outline indicate nest posts with a positive parasitism rate; points with a black outline and orange fill indicate posts where the parasitism rate was zero, and entirely black points indicate posts where the focal host taxon was not reared; therefore, parasitism rate could not be estimated. The gradient fill color reflects the parasitism rate. Nest post locations in chamise-dominated habitat are shown as triangles and those in oak-dominated habitat are shown as circles. Point size corresponds to host abundance. Full color version available electronically.

number of zero counts for this species and the greater availability of oak habitat at this site, this difference was not statistically significant (permutational ANOVA, $P = 0.682$).

In 2012, 333 eumenine wasps were collected from 14 nest posts using a different trapnest design. Eumenine abundance per post was significantly greater in chamise-dominated habitats (Fig. 5, permutational ANOVA, $P = 0.01152$). *Trypoxylon tridentatum* was uncommon in 2012, with only two individuals collected from a single post in oak-dominated habitat. However, 54 *Anthidium maculosum* bees were collected from 11 posts and 104 *Osmia lignaria* were collected from seven posts. *Anthidium maculosum* bees tended to be more abundant in chamise habitats, and *Osmia lignaria* was more common in oak habitats, though neither pattern was statistically significant (Fig. 5, permutational ANOVA; *Osmia lignaria*, $P = 0.4153$; *Anthidium maculosum* $P = 0.4755$).

In an analysis combining observations from all three years, *Anthidium maculosum* showed a significant preference for oak habitats (permutational ANOVA, $P = 0.0488$) and the abundance of Eumeninae was significantly greater in chamise habitats (permutational

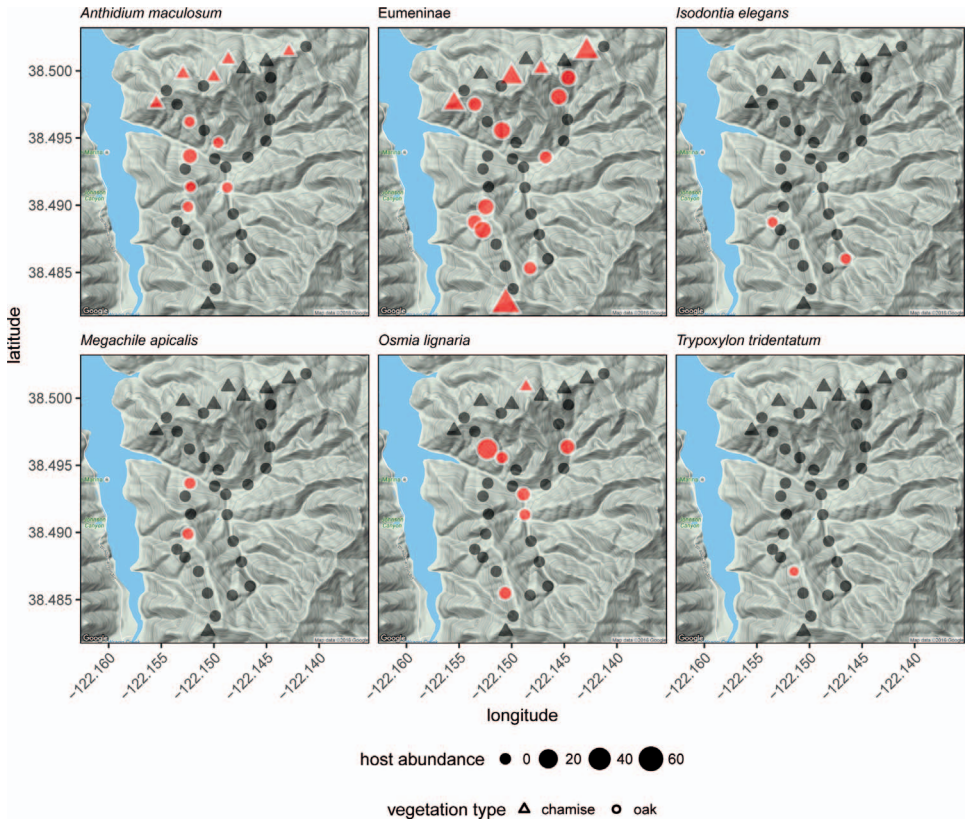


FIG. 5.—Spatial distribution of cavity-nesting taxa collected in 2012. Each point represents the location of a nest post containing 19 nesting tubes. Black points (without white outlines) mark locations where the focal taxon was not collected; red points (with white outlines) indicate locations where the focal taxon was collected. Post locations in chamise-dominated habitat are shown as triangles and those in oak-dominated habitat are shown as circles. Point size corresponds to host abundance. Full color version available electronically.

ANOVA, $P = 0.0336$). *Hoplitis albifrons maura* also showed a preference for chamise habitats, but this result was based only on collections in 2011, as previously reported.

The mean monthly temperature recorded for chamise-dominated habitats was consistently higher than that of oak-dominated habitats in all 3 y of the study. The largest difference in mean monthly temperature occurred in May, with chamise habitats averaging over 3 C hotter than oak habitats.

PARASITISM

We collected information on nest parasites from all reared taxa in 2011. Parasitism was not detected in *Isodontia elegans*, and was restricted to a small number of nest locations for *Hoplitis albifrons maura* and *Trypoxylon tridentatum*. In comparison, parasitism was common and widespread throughout the study region for Apoidea and Eumeninae (Table 1, and Figs

TABLE 1.—Parasitoid frequencies in 2011. Counts indicate the total number of host cells that were reared or parasitized. The overall parasitism rate was calculated as the total number of parasitized cells/ the total number of host cells reared for each host taxon

Taxon	Total reared cells	<i>Monodontomerus</i> spp.	Chrysididae	<i>Trichodes ornatus</i>	Other parasitoids	Total parasitized cells	Parasitism rate
Apoidea	46	24	0	0	2	26	0.565
Eumeninae	163	27	3	7	6	43	0.264
<i>Hoplitis albifrons maura</i>	31	3	0	0	0	3	0.097
Hymenoptera	26	1	12	0	2	15	0.577
<i>Isodontia elegans</i>	7	0	0	0	0	0	0.000
<i>Trypoxylon tridentatum</i>	37	0	1	0	0	1	0.027

4, 6). Of the 23 nest sites where eumenines were collected in 2011, 78% were parasitized ($n = 18$). The most common parasitoids observed in this study were *Monodontomerus* spp. (Torymidae). Based on specimens reared in 2011, we estimate that approximately 81% of these were *Monodontomerus torchioi*, with the remainder being a smaller unidentified species of *Monodontomerus*. The most common cleptoparasites were in the family Chrysididae (*Chrysis apontis*, *Chrysis inaequidens*, *Chrysis nitidula*, *Chrysura kyrae*, and *Caenochrysis deversor*). Less common members of the parasite community included five adult *Leucospis affinis* (Leucospidae) and seven adult *Trichodes ornatus* (Cleridae) reared in 2011. In 2011 the overall parasitism rate in Eumeninae was not significantly related to host density in this taxon (binomial GLM, $P = 0.5454$), but the rate of parasitism by *Monodontomerus* spp. showed a marginally significant positive relationship with host density (binomial GLM, $P = 0.0556$).

DISCUSSION

The results from our 3 y survey provide insight into a diverse solitary hymenopteran community with considerable variation in species distribution patterns, within-population temporal synchrony, and species composition influenced by spatial habitat heterogeneity.

Although changes in collection methodology preclude direct comparisons across the three years of this study, the monthly nest array collections in 2010 allowed for examination of within-year variation in nesting phenology and larval development. These collections indicate that for most taxa, larval development occurred in July and August, the period of the year with the highest daily mean and maximum temperatures in this region. Most taxa showed temporally restricted ranges, with at least 90% of all observations occurring within a single month for six of the eight taxa collected. In particular megachilid bees showed fairly distinct phenologies consistent with temporal niche separation; *Osmia lignaria* was collected primarily in the early-season, *Anthidium maculosum* was most abundant in the mid-season, and *Megachile apicalis* was a distinctly late-season species (Fig. 2). The temporal distributions of cavity-nesting bees and wasps at the reserve appear to be consistent with observed seasonal patterns in floral and caterpillar availability. However, a growing number of studies have documented phenological shifts across a diversity of plant and insect communities (e.g., Fitter and Fitter, 2002; Menzel *et al.*, 2006; Diamond *et al.*, 2011), including solitary hymenopterans (Bartomeus *et al.*, 2011). As the phenology of cavity-nesting bees and wasps changes in response to changing climatic conditions, variation in temporal range may have implications for population persistence. Taxa with longer periods of seasonal activity, such as *Trypoxylon tridentatum*, may be buffered against the risk of mismatch with nesting

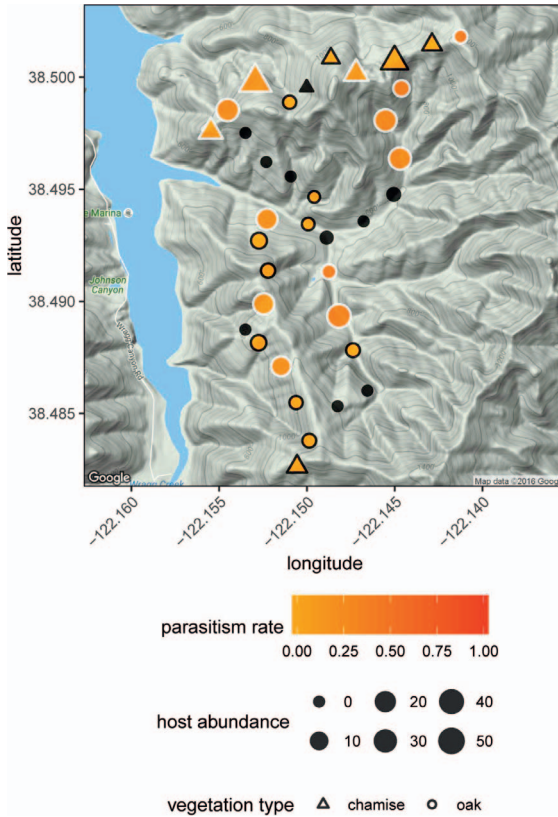


FIG. 6.—Spatial distribution of *Monodontomerus* spp. across all hosts in 2011. Point size indicates the total abundance of observed host taxa: Eumeninae, *Hoplitis albifrons maura*, unidentified Hymenoptera, and Apoidea. Points with a white outline indicate locations where a non-zero *Monodontomerus*-specific parasitism rate was measured; points with a black outline and orange fill indicate posts where the parasitism rate was zero, and entirely black points indicate posts where the focal host taxon was not reared. Therefore, parasitism rate could not be estimated. The color of the gradient fill indicates the parasitism rate. Post locations in chamise-dominated habitat are shown as triangles and those in oak-dominated habitat are shown as circles. Full color version available electronically.

resources. However, taxa with more limited temporal ranges (e.g., *Isodontia elegans*) may be more likely to develop phenological mismatch with prey used to provision their nests. Because we collected all nest tubes at monthly intervals regardless of whether they were completed and replaced them with empty tubes, it is possible that we displaced females that were in the process of nesting. Another possibility is that replacing completed nest tubes with empty tubes each month disrupted subsequent nesting in these aggregative hymenopterans. Therefore, a caveat to this portion of the study is the possibility that our monthly collections could underestimate the timespan over which some taxa were actively nesting.

In addition to differences in the timing of development, we found spatial distribution patterns across taxa. Eumenines (probably dominated by *Euodynerus foraminatus*, see *Natural history*) were widespread throughout the reserve and associated with both chamise-dominated and oak-dominated habitats in all 3 y of the survey (Figs. 3–5). In contrast a number of taxa, including *Isodontia elegans*, *Anthidium maculosum*, and *Megachile apicalis*, showed more limited and aggregated spatial distributions. For most species apparent preferences for oak- or chamise-dominated habitats were not statistically significant. One notable exception was the megachilid bee species *Osmia lignaria*, which showed a significant preference for oak-dominated habitats in 2010. It is possible that the dominant vegetation type provides an incomplete proxy for the wide range of abiotic and biotic factors that influence the abundance and distribution of these species. Specifically, differences in spatial distribution may be driven by variation in microclimate, competition with other cavity-nesting hymenopterans, proximity to water or soil resources, availability of floral or prey resources, and/or risk of parasitism.

Although solitary bees and wasps tend to nest in aggregations (Michener *et al.*, 1958; Rosenheim, 1990; Bosch, 1994), the proximate and ultimate causes of this behavior remain poorly understood. We examined whether these nesting aggregations might provide protection from parasitoids, resulting in reduced rates of parasitism. Based on our trapnest collections, the most abundant and widespread parasitoid in this system is *Monodontomerus torchioi* (Torymidae). According to previous research, *Monodontomerus* parasitoids appear to be highly attracted to olfactory cues emitted by host frass and cocoons (Filella *et al.*, 2011). We therefore expected parasitism rates to be highest at nest locations with high host densities because these locations were potentially most attractive to searching *Monodontomerus* females. Consistent with our expectations, we found a marginally significant positive relationship between eumenine host density and *Monodontomerus* spp. parasitism rate. These results suggest that nests with a higher density of eumenine hosts may be subject to higher rates of *Monodontomerus* parasitism than nests with lower host densities.

CONCLUSIONS

The results of this study highlight the spatial and temporal variation in the distribution of cavity-nesting hymenopteran taxa within an oak-chaparral landscape mosaic in California. Among the various taxa collected at Quail Ridge Natural Reserve, there were often clear differences in seasonal nesting phenology, population abundance, and nest site occupancy. Our results suggest that these spatial and temporal differences may be correlated with a suite of abiotic and biotic factors, including microclimate variation, surrounding vegetation type, and risk of parasitism. By aiming to disentangle these mechanisms, future studies may be able to provide a more comprehensive understanding of how this group of ecologically important insects varies across time and space.

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LITERATURE CITED

- ALCOCK, J., G. C. EICKWORT, AND K. R. EICKWORT. 1977. The reproductive behavior of *Anthidium maculosum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. *Behav Ecol Sociobiol.*, **2**:385–396.

PARASITIDS

- ANTONINI, Y., R. MARTINS, AND C. ROSA. 2003. Inverse density-dependent and density-independent parasitism in a solitary ground-nesting bee in Southeast Brazil. *Trop Zool.*, **16**:83–92.
- BARTHELL, J. F., J. M. HRANTZ, R. W. THORP, AND M. K. SHUE. 2002. High temperature responses in two exotic leafcutting bee species: *Megachile apicalis* and *M. rotundata* (Hymenoptera: Megachilidae). *Pan. Pac. Entomol.*, **78**:235–246.
- BARTOMEUS, I., J. S. ASCHER, D. WAGNER, B. N. DANFORTH, S. COLLA, S. KORNBLOTH, AND R. WINFREE. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci.*, **108**:20645–20649.
- BOSCH, J. 1994. Improvement of field management of *Osmia cornuta* (Latreille) (Hymenoptera, Megachilidae) to pollinate almond. *Apidologie*, **25**:71–71.
- COVILLE, R. 1986. Spider prey of *Trypoxylon tridentatum* (Hymenoptera: Sphecidae) from Arizona and California. *Pan. Pac. Entomol.*, **62**:119–120.
- DIAMOND, S. E., A. M. FRAME, R. A. MARTIN, AND L. B. BUCKLEY. 2011. Species' traits predict phenological responses to climate change in butterflies. *Ecology*, **92**:1005–1012.
- EBELING, A., A. M. KLEIN, W. WEISSER, AND T. TSCHARNTKE. 2012. Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia*, **169**:453–465.
- ENGELS, B. 2015. XNomial: Exact Goodness-of-Fit Test for Multinomial Data with Fixed Probabilities (R package). <https://cran.r-project.org/web/packages/XNomial/index.html>
- EVES, J. D. 1970. Biology of *Monodontomerus obscurus* Westwood, a parasite of the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Torymidae: Megachilidae). *Melandria*, **4**:1–18.
- FILELLA, I., J. BOSCH, J. LLUSIÀ, R. SEGO, AND J. PEÑUELAS. 2011. The role of frass and cocoon volatiles in host location by *Monodontomerus aeneus*, a parasitoid of Megachilid solitary bees. *Environ. Entomol.*, **40**:126–31.
- FITTER, A. H. AND R. S. R. FITTER. 2002. Rapid changes in flowering time in British plants. *Science*, **296**:1689–1691.
- FORMAN, R. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, United Kingdom. 609 p.
- FRANKIE, G., L. NEWSTROM, S. B. VINSON, AND J. F. BARTHELL. 1993. Nesting habitat preferences of selected *Centris* bee species in Costa Rican dry forest. *Biotropica*, **25**:322–333.
- FREEMAN, B. AND J. PARNELL. 1973. Mortality of *Sceliphron assimile* Dahlbom (Sphecidae) caused by the eulophid *Melittobia chalybii* Ashmead. *J. Anim. Ecol.*, **42**:779–784.
- FRICKE, J. M. 1991. Trap-nest bore diameter preferences among sympatric *Passaloeocus* spp. (Hymenoptera: Sphecidae). *Great Lakes Entomol.*, **24**:123–125.
- GATHMANN, A., H. J. GREILER, AND T. TSCHARNTKE. 1994. Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia*, **98**:8–14.
- GODFRAY, H. C. J. 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, N.J. 488 p.
- GOODELL, K. 2003. Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia*, **134**:518–527.
- GRISSELL, E. 2007. Torymidae (Hymenoptera: Chalcidoidea) associated with bees (Apoidea), with a list of Chalcidid bee parasitoids. *J. Hymenopt. Res.*, **16**:234–265.
- HASSELL, M. P. 1966. Evaluation of parasite or predator responses. *J. Anim. Ecol.*, **35**:65–75.
- HOLZSCHUH, A., I. STEFFAN-DEWENTER, AND T. TSCHARNTKE. 2009. Grass strip corridors in agricultural landscapes enhance nest-site colonization by solitary wasps. *Ecol. Appl.*, **19**:123–132.
- JENKINS, D. A. AND R. W. MATTHEWS. 2004. Cavity-nesting Hymenoptera in disturbed habitats of Georgia and South Carolina: nest architecture and seasonal occurrence. *J. Kansas Entomol. Soc.*, **77**:203–214.
- KEMP, W. P. AND J. BOSCH. 2005. Effect of temperature on *Osmia lignaria* (Hymenoptera: Megachilidae) prepupa-adult development, survival, and emergence. *J. Econ. Entomol.*, **98**:1917–1923.
- KRAEMER, M. E., F. D. FAVI, AND C. E. NIEDZIELA. 2014. Nesting and pollen preference of *Osmia lignaria lignaria* (Hymenoptera: Megachilidae) in Virginia and North Carolina orchards. *Environ. Entomol.*, **43**:932–941.

- KROMBEIN, K. 1967. Trap-nesting wasps and bees: life histories, nests, and associates, Smithsonian Press, Washington, D.C. 570 p.
- LARSSON, R. 1985. Individual size and nesting patterns in the gregarious digger wasp *Bembix rostrata* L. (Hymenoptera: Sphecidae). *Entomol. Tidskr.*, **106**:1-6.
- LOYOLA, R. D., AND R. P. MARTINS. 2006. Trap-nest occupation by solitary wasps and bees (Hymenoptera: Aculeata) in a forest urban remnant. *Neotrop. Entomol.*, **35**:41-48.
- MCCLURE, M. 1977. Parasitism of the scale insect, *Fiorinia externa* (Homoptera: Diaspididae), by *Aspidiotiphagus citrinus* (Hymenoptera: Eulophidae) in a hemlock forest: density dependence. *Environ. Entomol.*, **6**:551-555.
- MENZEL, A., T. H. SPARKS, N. ESTELLA, E. KOCH, A. AASA, R. AHAS, K. ALM-KUBLER, P. BISSOLLI, O. BRASLAVSKÁ, AND A. BRIEDE. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biol.*, **12**:1969-1976.
- MICHENER, C. D. 1947. A character analysis of a solitary bee, *Hoplitis albifrons* (Hymenoptera, Megachilidae). *Evolution*, **1**:172-185.
- , R. B. LANGE, J. J. BIGARELLA, AND R. SALAMUNI. 1958. Factors influencing the distribution of bees' nests in earth banks. *Ecology*, **39**:207-217.
- MINCKLEY, R. L., J. H. CANE, AND L. KERVIN. 2000. Origins and ecological consequences of pollen specialization among desert bees. *Proc. R. Soc. B*, **267**:265-271.
- MORRISON, G. AND D. R. STRONG. 1980. Spatial variations in host density and the intensity of parasitism: some empirical examples. *Environ. Entomol.*, **9**:149-152.
- O'NEILL, K. M. 2001. Solitary wasps: behavior and natural history. Cornell University Press, Ithaca, N.Y. 406 p.
- AND R. P. O'NEILL. 2007. Nests and prey of *Isodontia elegans* (F. Smith) (Hymenoptera: Sphecidae) in Montana, USA. *Entomol. News*, **118**:139-142.
- POLIDORI, C., R. BOESI, AND W. BORSATO. 2011. Few, small, and male: Multiple effects of reduced nest space on the offspring of the solitary wasp, *Euodynerus* (Pareuodynerus) *posticus* (Hymenoptera: Vespidae). *C. R. Biol.*, **334**:50-60.
- POTTS, S. G., B. VULLIAMY, S. ROBERTS, C. O'TOOLE, A. DAFNI, G. NEEMAN, AND P. WILLMER. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.*, **30**:78-85.
- R CORE TEAM. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- ROSENHEIM, J. A. 1990. Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Ann. Entomol. Soc. Am.*, **83**:277-286.
- SOBEK, S., T. TSCHARNTKE, C. SCHERBER, S. SCHIELE, AND I. STEFFAN-DEWENTER. 2009. Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecol. Manage.*, **258**:609-615.
- STAHLHUT, J.K. AND D. P. COWAN. 2004. Inbreeding in a natural population of *Euodynerus foraminatus* (Hymenoptera: Vespidae), a solitary wasp with single-locus complementary sex determination. *Mol. Ecol.*, **13**:631-638.
- STEFFAN-DEWENTER, I. AND K. LESCHKE. 2003. Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodivers. Conserv.*, **12**:1953-1968.
- AND S. SCHIELE. 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology*, **89**:1375-1387.
- THORNE, J. H., KENNEDY, J. A., QUINN, J. F., MCCOY, M., KEELER-WOLF, T., AND MENKE, J. A. 2004. Vegetation map of Napa County using the manual of California vegetation classification and its comparison to other digital maps. *Madrono: West Am. J. Botany*, **51**:343-363.
- THORP, R. W. 1969. Ecology and behavior of *Anthophora edwardsii* (Hymenoptera: Anthophoridae). *Am. Midl. Nat.*, **82**:321-337.
- TORCHIO, P. F. 1989. Biology, immature development, and adaptive behavior of *Stelis montana*, a cleptoparasite of *Osmia* (Hymenoptera: Megachilidae). *Ann. Entomol. Soc. Am.*, **82**:616-632.

- TORCHIO, P. F. AND V. J. TEPEDINO. 1980. Sex ratio, body size and seasonality in a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). *Evol.*, **34**:993–1003.
- TURCHIN, P. AND P. KAREIVA. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology*, **70**:1008–1016.
- TYLIANAKIS, J. M., A.M. KLEIN, AND T. TSCHARNTKE. 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*, **86**:3296–3302.
- VINSON, S. B. AND G. W. FRANKIE. 1988. A comparative study of the ground nests of *Centris flavifrons* and *Centris aethiocesta* (Hymenoptera: Anthophoridae). *Entomologia Experimentalis et Applicata*, **49**:181–187.
- VINSON, S. B., G. W. FRANKIE, AND R. E. COVILLE. 1987. Nesting habits of *Centris flavofasciata* Friese (Hymenoptera: Apoidea: Anthophoridae) in Costa Rica. *J. Kansas Entomol. Soc.*, **60**:249–263.
- WCISLO, W. T. 1984. Gregarious nesting of a digger wasp as a “selfish herd” response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sarcophagidae). *Behav. Ecol. Sociobiol.*, **15**:157–160.
- 1986. Host nest discrimination by a cleptoparasitic fly, *Metopia campestris* (Fallen) (Diptera: Sarcophagidae: Miltogramminae). *J. Kansas Entomol. Soc.*, **59**:82–88.
- ZEILEIS, A., C. KLEIBER, AND S. JACKMAN. 2008. Regression models for count data in R. *J. Stat. Softw.*, **27**:1–25.

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