

RESOURCE DISTRIBUTIONS AMONG HABITATS DETERMINE SOLITARY BEE OFFSPRING PRODUCTION IN A MOSAIC LANDSCAPE

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Abstract. Within mosaic landscapes, many organisms depend on attributes of the environment that operate over scales ranging from a single habitat patch to the entire landscape. One such attribute is resource distribution. Organisms' reliance on resources from within a local patch vs. those found among habitats throughout the landscape will depend on local habitat quality, patch quality, and landscape composition. The ability of individuals to move among complementary habitat types to obtain various resources may be a critical mechanism underlying the dynamics of animal populations and ultimately the level of biodiversity at different spatial scales. We examined the effects that local habitat type and landscape composition had on offspring production and survival of the solitary bee *Osmia lignaria* in an agri-natural landscape in California (USA). Female bees were placed on farms that did not use pesticides (organic farms), on farms that did use pesticides (conventional farms), or in seminatural riparian habitats. We identified pollens collected by bees nesting in different habitat types and matched these to pollens of flowering plants from throughout the landscape. These data enabled us to determine the importance of different plant species and habitat types in providing food for offspring, and how this importance changed with landscape and local nesting-site characteristics. We found that increasing isolation from natural habitat significantly decreased offspring production and survival for bees nesting at conventional farms, had weaker effects on bees in patches of seminatural habitat, and had little impact on those at organic farm sites. Pollen sampled from nests showed that females nesting in both farm and seminatural habitats relied on pollen from principally native plant species growing in seminatural habitat. Thus connectivity among habitats was critical for offspring production. Females nesting on organic farms were buffered to isolation effects by switching to floral resources growing at the farm site when seminatural areas were too distant. Overall local habitat conditions (farm management practices) can help bolster pollinators, but maintaining functional connectivity among habitats will likely be critical for persistence of pollinator populations as natural habitats are increasingly fragmented by human activities.

Key words: *agro-ecosystem; connectivity; habitat fragmentation; landscape change; native bees; Osmia lignaria; reproduction; resource distribution.*

INTRODUCTION

The fragmentation and loss of native habitat resulting from human activity are two of the primary factors contributing to declines of native species worldwide (Wilcove et al. 1998, Harrison and Bruna 1999) and to profound changes in ecological functioning (e.g., Didham et al. 1998, Crooks and Soule 1999, Cunningham 2000, Laurance and Williamson 2001, Donaldson et al. 2002). Most studies of biodiversity and landscape change have focused on differences in species richness or composition among sites (i.e., the community level) or have explored numerical responses of populations (Debinski and Holt 2000), with results that vary from strongly negative to positive (reviewed in Tischendorf et al. 2005). Less is known about the mechanistic basis

underlying population response to habitat or landscape change (McGarigal and Cushman 2002, Tischendorf et al. 2005). For example, do reproduction and survival differ among habitat types (e.g., Pulliam 1988, e.g., Gundersen et al. 2001), and are such differences determined by the distribution of resources in the landscape and the ability of individuals to access them? Because the responses of individual species underlie community patterns, understanding the mechanistic basis of species-specific responses to landscape change may help to explain the variability in community scale outcomes. Species that rely on discrete patches of a single habitat type within a larger matrix (Schultz and Crone 2001, Wolf and Harrison 2001) will respond differently from those that use resources from the matrix or for whom the landscape is a mosaic of habitats providing complementary resources and differential mortality risks (Dunning et al. 1992, Brommer and Fred 1999, Lindenmayer et al. 2003, Westphal et al. 2003, Lin and Batzli 2004).

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For many species, population dynamics are determined by factors operating at a variety of spatial and temporal scales from local (single patch) to landscape (e.g., composition and connectivity of habitats; Levin 1992, McGarigal and Cushman 2002). This characteristic necessitates investigation across multiple scales. In this paper, we report on the influence of local site and landscape characteristics to offspring production by a species of solitary bee (*Osmia lignaria* Say) and identify the importance of resources collected from different habitat types to nest establishment and fecundity within an agri-natural landscape.

Agriculture is the leading form of human land use worldwide and the largest cause of native habitat loss and fragmentation (Defries et al. 2004). Agricultural intensification at single sites and across landscapes has led to declines in diversity and abundance of many taxa (Donald et al. 2001, Benton et al. 2002, Tscharntke et al. 2005). However, in agricultural areas that include mosaics of natural and managed habitats and where on-site farming practices are less intensive, significant biodiversity can be maintained within the system (Perfecto and Vandermeer 2002, Tscharntke et al. 2005). The global dominance of agro-ecosystems in terrestrial realms (Matson et al. 1997, Vitousek et al. 1997, Tilman et al. 2001, MEA 2005) means that populations of many species exist at the interface of agricultural and natural areas or within agricultural landscapes. This highlights the need for greater attention to how populations and communities function, and what factors affect species persistence within these landscapes.

Several attributes of bees' biology make them well suited to explore the roles of local and landscape factors in population persistence in fragmented systems. Bees are central-place foragers with nests that exist in identifiable habitat types, allowing for exploration of the effect of nesting habitat on survival and reproduction (Goulson et al. 2002). Nonetheless, the persistence of bee populations, like those of many other animal species, may rely on the ability of individuals to move among patches. Bees require distinct types of resources, including nesting substrates, nesting material, and floral resources. The distributions of these resources vary among habitat types over space and over time (Westrich 1996). Thus landscape level factors, such as the amount and distribution of various habitat types, the resources they contain, and connectivity among habitat types, could be critical to maintaining bee populations. Where landscapes are patchworks of natural and human-dominated land, spatial and temporal variation in resource abundance and distribution are likely to be accentuated. In agricultural areas various native plants flower throughout the season in remnants of natural habitat, while crops bloom in pulses at differing times (Kremen et al. 2002a, Westphal et al. 2003). Bees nesting in the fallow margin of a field might forage in patches of natural habitat at one time and at a crop field during

another. With the exception of managed honey bees and bumble bees, few studies have quantified bees' use of different habitats and the plant species they contain (Bowers 1985, Rasheed and Harder 1997, Goulson et al. 2002, Villanueva 2002).

Studies from throughout the world indicate that landscape fragmentation and degradation often lead to declines in diversity and abundance of insect pollinators as well as pollination (Aizen and Feinsinger 1994, Cunningham 2000, Aizen et al. 2002, Klein et al. 2002, Kremen et al. 2002b, Steffan-Dewenter et al. 2002, Klein et al. 2003, Ricketts 2004); however, some studies have recorded exceptions (Aizen and Feinsinger 1994, Cane and Tepedino 2001, Donaldson et al. 2002). This variability suggests that response may depend on life history and other species-specific attributes (Rathcke and Jules 1993, Cane and Tepedino 2001) or on specific characteristics of the studied landscapes. Here we report on several factors that may determine the direction and magnitude of such patterns. We show the degree to which the type of habitat in which bees were nesting and the abundance of resources at the nesting site (local factors) vs. isolation of nests from seminatural habitat (landscape/foraging-scale factor) affected offspring production and offspring survival for the solitary bee *O. lignaria*. Offspring production is a central component of population growth, and ours are the only such data for any bee species to be measured in the context of both local nesting site and landscape factors (but see Goulson 2002). Small changes in offspring number may have particularly dramatic effects on population persistence for solitary bees because of their low reproductive rate compared to many other insects (Tepedino and Parker 1983, Danforth 1990, Torchio 1990). We also identified pollen species collected by female bees and mapped the abundances of corresponding plants in different habitats within the landscape. This allowed us to identify the plant species used by *O. lignaria* and estimate foraging movements within and among habitats as the composition of the landscape changed. The time and energy required to gather resources may be an important mechanism underlying offspring production and thus help to reveal the causes of a species' sensitivity to landscape change.

METHODS

Study species and system

The native bee *Osmia lignaria propinqua* Say is a trophic generalist, collecting pollen from species in at least 18 plant families (Rust 1974, Cripps and Rust 1989). Females nest in existing holes in dead wood (e.g., old beetle burrows) and construct nests as a linear series of brood chambers. Each chamber is provisioned with pollen and nectar, atop which a single egg is laid. The nest records both a temporal sequence of offspring production (oldest at the rear) and pollen use. Females readily nest within holes drilled into wood blocks. Such blocks of artificial nest sites can be placed at specific

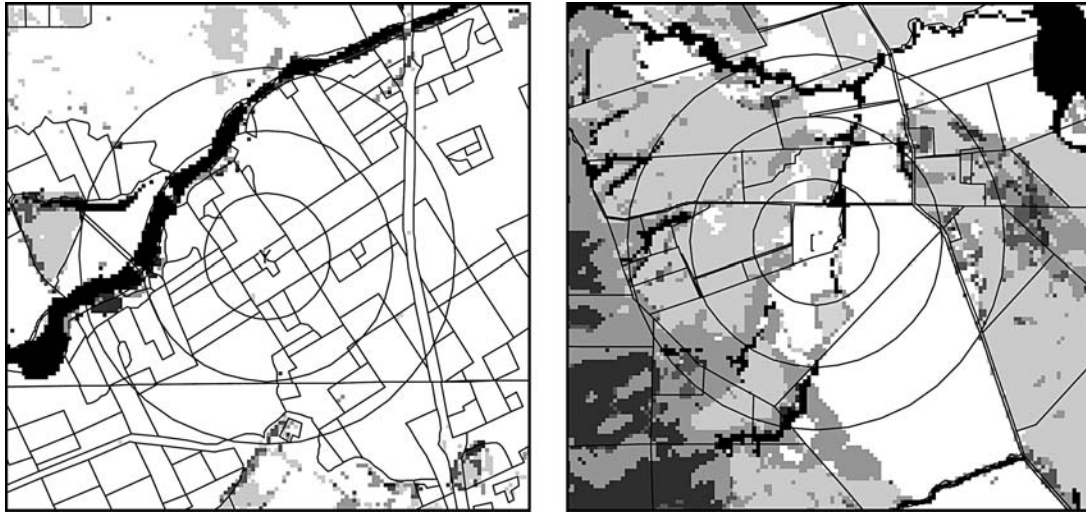


FIG. 1. Two nesting sites in different landscapes: (A) an organic site surrounded primarily by row crop agriculture and (B) a conventional farm site surrounded by native and row crop habitat. Circular buffers are at 0.5, 1.0, and 1.5 km around the nest location. White indicates row crop or orchard; gray shows upland native habitat; black shows riparian habitat.

locations within the landscape and used to monitor nesting by individuals. In this study we lined the nest holes with paper tubes (Tepedino and Torchio 1982b), which allowed us to remove active nests temporarily and record nesting progress. Straws also facilitated pollen sampling from completed nests (e.g., Williams and Tepedino 2003).

The study landscape, in Yolo County and Solano County, California, USA, was a mixture of row and orchard crops interspersed with seminatural habitats (Fig. 1). Seminatural habitats included chaparral, oak woodland, and riparian areas (Kremen et al. 2004). The landscape has a distinct west-to-east gradient of increasing agricultural intensification, with primarily seminatural areas in the foothills of the coastal range and an increasing agricultural land eastward into the Central Valley.

Study design

To explore local and landscape scale effects of agricultural intensification on offspring production, flower use, and foraging movement within and among habitats, we established 30 study sites along the landscape gradient. Among all sites, elevation changed <120 m, and daily mean temperatures were within 2°C. Each site was separated by at least 1.5 km from its nearest neighbor and was located on either a conventional or organic farm or in riparian vegetation. Conventional farms differed from organic farms by planting crop monocultures, applying bee-toxic pesticides, and using a weed-free tillage regime. Riparian habitat supported mixtures of native plants including *Salix* spp., *Cercis occidentalis*, *Baccharis salicifolia*, and a variety of weedy exotics (e.g., *Arundo donax*, *Tamarix* spp., *Brassica nigra*). All sites were on at least 3 ha of the focal habitat type.

Our land-use gradient paralleled a strong spatial gradient. Care was therefore taken whenever possible to replicate each local site type along the spatial/land-use gradient. Tests of the main response variables (per capita offspring production, offspring survival, and nest establishment) showed no evidence for spatial autocorrelation. There was no correlation between geographic distances and offspring production (Mantel $r = 0.065$, $P = 0.13$) or survival (Mantel $r = 0.089$, $P = 0.08$). For nest establishment, the initial test for spatial autocorrelation was significant (Mantel $r = 0.158$, $P = 0.04$), but this proved to be due to the landscape predictor variable (isolation from natural habitat) rather than geographic distance; a partial Mantel test factoring out the isolation was not significant (Mantel $r = 0.021$, $P = 0.34$; R Program, Version 4.0, Casgrain and Legendre 2004).

We used a Geographic Information System (GIS) land classification based on Landsat data at 30-m resolution to measure landscape characteristics for each site. The GIS habitat classification was corrected based on ground-truthing during two successive seasons and is judged to be 96% accurate in distinguishing between agricultural and seminatural riparian and upland habitat, which includes oak woodland, chaparral, and grasslands (Kremen et al. 2004). In preliminary analysis we separated riparian from the upland habitats, because nests were placed within riparian habitat. Isolation from riparian habitat had a weaker effect on offspring production, but trends were congruent with those based on upland and all seminatural habitats pooled. For final analysis we grouped riparian and upland as seminatural habitat and combined all crop types as agricultural habitat. Organic farms composed a small fraction of the landscape and were not clearly separable in the GIS. They were therefore lumped with other agriculture for the landscape scale analysis.

At each site we placed pairs of wooden blocks, each containing 18 nest holes of the appropriate size for *O. lignaria* (Tepedino and Torchio 1989). In each block-pair we put 12 preemergent female and 15–20 male *O. lignaria* still within their cocoons. These individuals were collected from nests made the previous season and their sex determined by X-ray of the cocoons (Tepedino and Torchio 1982b). All were obtained from a single region. This “seeding” of the nests with bees increased the probability that we would obtain sufficient nesting females to monitor. Nests were set out between 5 March and 8 March, one week prior to the time when *O. lignaria* typically emerges in this region, and matched with the phenology of plants on which the earliest *O. lignaria* had been collected in past seasons (N. M. Williams and C. Kremen, *unpublished data*). Bees from our nests emerged over the next 10 d. We checked nests for emergence and substituted additional preemergent individuals for those that died in cocoon so that the numbers emerging were consistent among all sites.

We monitored all nests every third flight day, after placing blocks in the field, and recorded nest initiation and progress until nesting activity ceased (32 calendar days). Flight days were those on which the temperature in the study area exceeded 12°C (minimum for *O. lignaria* flight; Bosch and Kemp 2002) for 5 h and on which there was no precipitation for at least two-thirds of the daylight hours. On each monitoring day, we marked nesting progress on the straw insert so that pollen samples associated with a specific date could later be collected (Williams and Tepedino 2003). We measured offspring production as the number of cells provisioned within a nest during the flight season, and we equated survival of offspring with emergence the following spring. Because our measure is based on nests, it could underestimate individual female fecundity if females made multiple nests (Tepedino and Torchio 1982a).

On each date that we monitored nesting we also assessed the abundance of flowers for all plant species within 100 m of the nest block. Abundance was estimated as a series of categories: 1–9, 10–99, 100–999, 1000–4999, 5000–9999, 10 000–49 999, and >50 000 flower units at the site. Because we monitored offspring production for a small number of individuals in the bee community and do not know the exact foraging ranges of any individual, it is unlikely that a bee’s reproductive output would be related to small differences in flowering density (Williams and Tepedino 2003). Thus our categories were intended to capture substantial differences in availability of resources among sites. Flower units were chosen to be reliably countable and were defined on a species-by-species basis either as a flower (e.g., *Prunus* spp.) or inflorescence (*Salix* spp.). Such units are directly comparable among sites but not among species; our goal was to compare among sites throughout the landscape.

To determine the species of pollen used by females, we sampled pollen from two randomly selected provisions completed during each 3-d period per site. This provided 16 samples per nest location during the month-long foraging season, except for when females at that site had not initiated nests by the first sampling date or had ceased nesting before the final period. We sampled pollen using sterile, fine-tipped forceps, which allowed >10⁴ grains to be sampled (still a small fraction of the total provision). The nests were resealed following pollen sampling so that larvae could complete development. This procedure does not appear to affect larval growth or survival (N. M. Williams, *unpublished data*).

Pollen samples were acetolyzed (Erdtman 1969), and the proportion of each pollen species was then scored from a sample of 300 grains, using a compound light microscope. This proportion was used as the metric of pollen use. We based identifications on a pollen reference collection of all flowering plant species from the study area. We could not reliably distinguish among the *Salix* species (predominantly *S. laevigata* and *S. exigua*, with a lesser amount of *S. sessilifolia*), *Lupinus* species (*L. benthami*, *L. succulentus*, and at some sites *L. microcarpum*), *Malus* varieties, or *Prunus* species, and we pooled species within each group for analyses. Herbarium specimens of plants are deposited at the University of California–Davis herbarium, and pollen specimens and digitized photos are maintained as a reference collection at Bryn Mawr College.

Analyses

We compared nesting success and offspring production among local site types and as a function of the landscape using ANCOVA (SAS PROC GLM, Version 8.2, SAS Institute 2001). For the landscape variable, we used values of the index

$$H_x = \sum_{i \neq x} A_i e^{-\frac{d_i}{D}}$$

which is a standard metric of the proximity/isolation of a given location relative to habitat patches within the landscape. The index is essentially a distance-weighted measure of the area of a particular habitat surrounding the focal location. A_i is patch area for all patches of the designated habitat type, d_i is the distance to patch i , and D is a species-specific mobility constant equal to one-half the mean foraging distance (Moilanen and Nieminen 2002, Winfree et al. 2005). All distances and areas were measured in meters. Distances were measured from nest block to nearest edge of the patch using ArcGIS, Version 9.0 (Environmental Systems Research Institute, Redlands, California, USA). Offspring production is in part a function of energy and time expended during foraging, which for a central-place forager like *O. lignaria* depend on the distance to and abundance of resources in the landscape (Orians and Pearson 1979). To the extent that larger patches of natural habitat contain more abundant and diverse resources, the index,

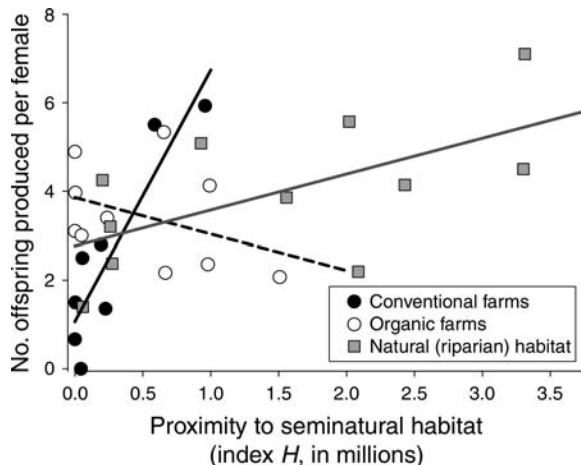


FIG. 2. Mean number of offspring produced per female at each study site. Lines show least-squares fits for each habitat type as a function of proximity/isolation index values H (see *Methods: Analyses*), where H (unitless) can be intuitively interpreted as the distance-weighted area of seminatural habitat surrounding the site; area was measured in m^2 . The values of index H are in millions. Note that the partial regression coefficient is the slope of a line fit to data with H on the x -axis and the different listed variables in Table 1 on the y -axis. The change in number of offspring is therefore tiny (a fraction of an offspring) for a unit of change in H .

which incorporates distance to and area of patches, should be indicative of the spatial distribution and net value of resources in the foraging landscape. We defined patches as areas of seminatural habitat in our GIS landscape layer of at least 0.36 ha (four grid cells). Patches of this size reliably matched habitat types based on ground-truthing and were large enough to contain characteristic vegetation. Altering the patch size cutoff across a range from 0.27 ha to 0.54 ha did not change the results of our analysis.

Insect movement can vary in different landscapes and habitat types (Ricketts 2001). We therefore investigated the best scale prior to completing a full analysis of our data. We calculated the index H_D for D values from 25 m to 1500 m using patch areas and distances taken within 1.5 km of the site where nests were placed. The 1.5-km maximum was used because this represents a maximum recorded foraging distance for *O. lignaria* (Rust 1990) and far exceeds observed typical foraging distances and projected distances based on body size (S. A. Greenleaf et al., *unpublished manuscript*). We then ran a series of regressions between offspring production and all H_D values, including site type in the model (Steffan-Dewenter et al. 2002, Holland et al. 2004). R^2 increased sharply at D values between 360 m and 500 m and remained consistent at larger scales. Such a jump in explanatory power may be indicative of a scale at which the species perceives that landscape. These D values correspond to foraging distances of 720–1000 m, which are consistent with observed foraging distances (Rust

1990). We completed subsequent analyses of landscape level using $D = 500$ m.

When analyses showed significant site type \times isolation interactions we compared the local site effect at two different regions of the isolation gradient, using a natural break in the gradient to divide into NEAR sites (these correspond to sites with 21–70% seminatural habitat within 1000 m of the nest) and FAR sites (seminatural habitat comprised <20% of the surrounding area). Interaction precludes interpretation of the local habitat effect based on the simple ANCOVA; thus splitting the gradient allowed us to examine the dependence of local habitat factor on the landscape context.

To test the effect of local resource availability on offspring production we calculated rank correlations between number of offspring per nest and aggregate flower abundance among sites, including only those plant species whose pollens were collected by *O. lignaria*. We also tested whether availability of a given species affected the collection of its pollen, using separate rank correlations between floral abundance and pollen use for each of the four species that dominated *O. lignaria* provisions. Finally we tested how use of these four pollens changed across the landscape using, multivariate multiple regression with proximity index as a continuous effect and site type as a fixed effect (SAS PROC GLM, SAS Institute 2001). The pollen use variable received an angular transformation to improve normality.

We investigated the movement of foraging females among habitat types and the reliance of offspring production on resources from sites/habitat types beyond that on which nests were located. Based on the identity of flowering plants at each site and a pollen reference collection, we calculated the portion of the pollen sampled from each nest that likely originated from plants growing on site vs. off site, for all nesting sites along the landscape gradient. We ran separate analyses for nests in each habitat type. Where ambiguous, we attributed pollen to on-site sources, so our measure of reliance on other habitats in the landscape is conservative.

RESULTS

Landscape and local habitat effects

Isolation of the nesting site from seminatural habitat strongly affected per capita offspring production, but the effect depended on the local habitat in which a bee's nest was located (habitat type \times isolation interaction $F_{2,23} = 9.12$, $P = 0.001$; Fig. 2). For riparian and conventional farm sites, offspring production decreased with isolation from seminatural habitat surrounding the site (partial regression β significance, $t = 4.29$, $P < 0.001$, $t = 2.61$, $P = 0.02$); however, on organic farms, the degree of isolation did not significantly affect offspring production ($t = 1.09$, $P = 0.29$; Fig. 2). When there were differences in number of offspring produced per female among sites, these resulted from different rates of cell

TABLE 1. Results from ANCOVA for various measures related to offspring production as a function of isolation from natural habitat and local site type.

Measure	R^2	P	Conventional farm	Organic farm	Riparian habitat
Total cells provisioned	0.59	<0.001	5.67 (0.003)	-0.82 (0.28)	0.81 (0.02)
Cells provisioned per day	0.53	0.002	0.48 (0.002)	-0.09 (0.23)	0.08 (0.014)
Nesting duration	0.20	0.23†			
Surviving offspring	0.41	0.028	3.92 (0.026)	-1.7 (0.24)	0.58 (0.13)
Nests established	0.56	0.001	4.8 (0.006)	-0.08 (0.39)	1.36 (0.004)

Notes: R^2 and significance levels are provided for each full model. The remaining values are partial regression coefficients β ($\times 10^{-6}$) of response to isolation from natural habitat, with P values in parentheses.

† This value is pooled, rather than based on a specific habitat type; the pooled estimate of the slope is -0.005, with $P = 0.79$ for that slope. There was no significant site type \times isolation interaction in the model.

provisioning rather than from differences in nesting duration, which did not differ among habitat types or with landscape structure (Table 1). The numbers of offspring surviving to adulthood showed the same pattern as for per capita offspring production, except that the effect of landscape was significant only for bees nesting at conventional farm sites (Table 1).

The number of successful nests established at the site also paralleled the results for per capita offspring production (Table 1). On conventional farms and in riparian habitats the number of females that established nests decreased with isolation from native habitat. At organic farms nest establishment did not depend on the amount and proximity of native habitat surrounding the site. Our metric of nest establishment includes not only the nesting success of individuals we placed at the site, but potentially that of females that either emerged nearby naturally or dispersed to the site. Thus differences in the abundance of resident *O. lignaria* females across the landscape gradient may accentuate the patterns observed. This was certainly the case at one riparian site that had 24 females nesting in the blocks; all other sites had between one and eight nesting females. The pattern of nesting was consistent whether or not we included this extreme site, and we excluded it as an outlier in our final analysis.

The effect of local site type on offspring production depended on the proximity of the site to natural habitat (Fig. 2). Per capita offspring production, offspring survival, and nest establishment did not differ among site types for sites NEAR to natural habitat (Fig. 3A). Among the FAR sites, however, bees nesting on organic farms produced significantly more offspring, and more of these survived than for bees on conventional farms (Fig 3B). Those nesting in riparian habitats produced an intermediate number.

Pollen use

Osmia lignaria collected pollen from 19 plant species, although most of these represented small fractions of the provisions (see Appendix). Females nesting in all habitat types collected pollen from predominantly four species groups, all of which were native: *Cercis occidentalis*,

Salix spp., *Quercus lobata*, and *Lupinus* spp. On average, these pollens accounted for 81–100% of provisions sampled. At some of the more isolated farm sites females collected substantial amounts of *Prunus domestica* (plum) or *Fragaria ananassa* (strawberry) as well as native plants that grew in remnant or restored habitat on the farm site. For example, provisions at the most isolated organic farm site contained *P. domestica*, *Malus* spp. (combined 34.1%), *Ceanothus oliganthus* (33.4%, growing in a restored hedgerow planting), *Salix* spp. (19%), *F. ananassa* (5.8%), and cultivated *Brassica/Raphanus* spp. (3.1%). Although such pollens were never dominant among all farms, they were important resources at some organic farm sites. Additional minor species within the provisions varied more dramatically among sites, but always comprised <8% of sampled pollen at a site.

The amounts of the four predominant pollen species collected differed significantly among site types (Wilks' $\lambda = 0.467$, $F_{8,42} = 2.43$, $P < 0.03$; Fig. 4). Use of *Salix* decreased and *C. occidentalis* increased with proximity of the site to natural habitat. *Quercus* use remained

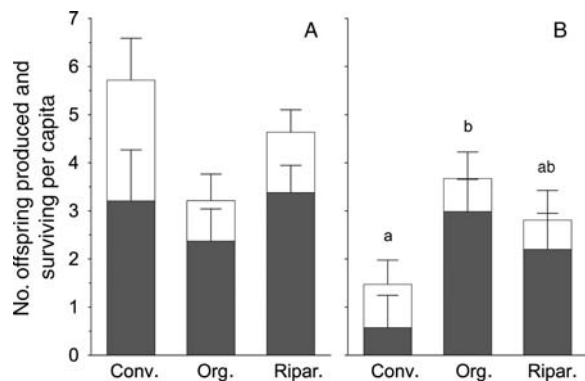


FIG. 3. Mean (+SE) number of offspring provisioned (total bar) and surviving to emergence (gray portion) at the three habitat types (conventional farms, organic farms, riparian habitat) for (A) NEAR sites (less isolated) and (B) FAR sites (more isolated). Different lowercase letters indicate significant differences among means ($P = 0.05$ for offspring produced; $P = 0.1$ for survival). Both P values are Bonferroni adjusted.

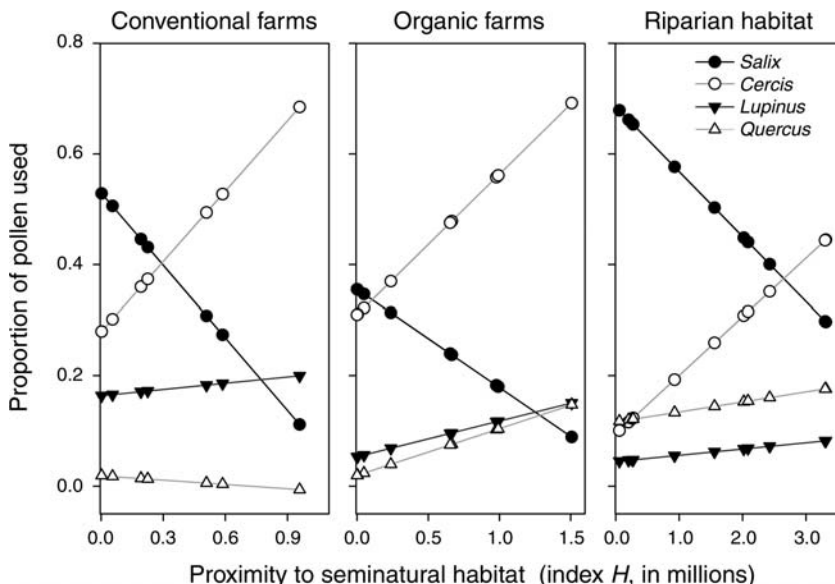


FIG. 4. Mean pollen use by females nesting in different habitat types and as a function of isolation of the nest from natural habitat. Values are least-square means from univariate multiple regression of each pollen species following a multivariate MANOVA among all pollens, habitat types, and degree of isolation. Sites that are more isolated fall toward the origin. Index values (H) are calculated as in Fig. 2. Pollen use did not vary significantly with date, and data are averages for the month-long season. The y -axis represents the proportion of pollen grains used (collected by a female bee) out of the total counted in a sample.

relatively constant. The use of *Lupinus* spp. depended strongly on the vegetation surrounding the individual site rather than on isolation.

Resource availability

Focusing only on plant species whose pollens were collected by *O. lignaria*, the amount of these resources that were available at the nesting site differed among site types (Fig. 5). Riparian sites had substantially more

total resources than organic farms, although the difference was not significant. Both had significantly more resources than conventional farm sites: riparian $100\,700 \pm 96\,700$ flowers per site (mean and 95% CI, $n = 11$); organic farm $8200 \pm 101\,400$ flowers per site, $n = 10$; conventional farm $1099 \pm 113\,400$ flowers per site, $n = 8$. Only three of eight conventional farms had any plant species used by *O. lignaria* compared to nine of 10 organic farm sites. The abundance of flowers at the

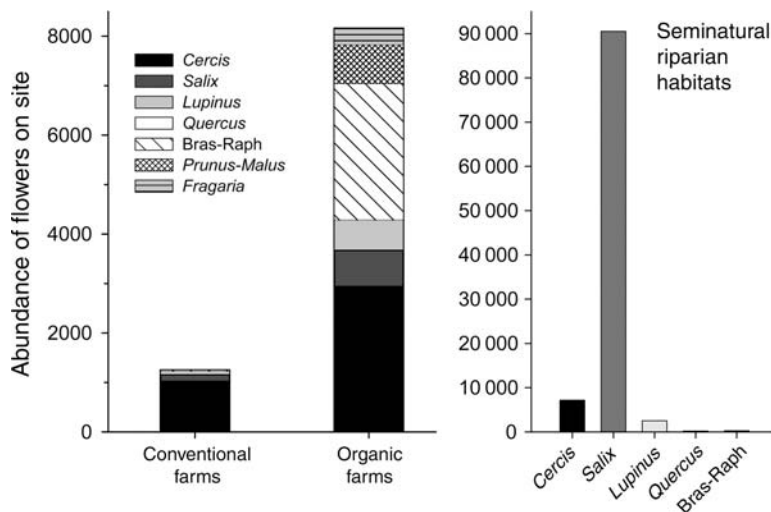


FIG. 5. Total flower abundance (number of flowers) of the primary species used by *O. lignaria* at each habitat type. Data are averages across all sites. Total abundance at each site was measured for flowers within ~ 100 m of the nest location. “Bras-Raph” is the combined total for cultivated *Brassica* and *Raphanus* species; *Prunus-Malus* is the combined total for cultivated species of *Prunus* and *Malus*.

nesting site did not significantly correlate with proximity to seminatural habitat (conventional farm, Kendall $\tau = 0.60$, $P = 0.06$, $n = 8$; organic farm $\tau = 0.22$, $P = 0.46$, $n = 11$; riparian $\tau = 0.22$, $P = 0.25$, $n = 11$), although there was a positive trend on conventional farms. The trend emerged because the three conventional sites containing plants species used by *O. lignaria* were the least isolated ones. In contrast, *Salix* spp. flowered at all riparian sites, and *Ceanothus oliganthus*, *Lupinus* spp., or *Quercus* grew at some of the organic farms throughout the landscape gradient.

The availability and proximity of resources significantly affected the numbers of offspring produced by *O. lignaria*; however, the effect was not a straightforward function of flowers growing at the nest site (on-site resources). Offspring production did not correlate with the abundance of flowers at the nesting site (assessed within a 100 m radius) for any of the habitat types (Kendall τ , conventional farm $\tau = 0.32$, $P = 0.31$, $n = 8$; organic farm $\tau = 0.05$, $P = 0.82$, $n = 11$; riparian $\tau = 0.11$, $P = 0.64$, $n = 11$).

Comparison of on-site and off-site pollen use (as inferred by the presence or absence of these plant species within a 100 m radius of nest sites) revealed an underlying cause of the patterns of offspring production along the landscape gradient. Bees nesting on conventional farm sites collected almost no pollen from plants flowering at the nesting site because almost nothing was flowering at these sites. The exception was the least isolated site where *Salix* was in flower and was collected in large amounts (Fig. 6). In contrast, bees nesting at organic sites collected substantial amounts of pollen from the nesting site; however, their use of on-site resources decreased along the gradient from more isolated to less isolated, such that bees near seminatural habitats used mostly off-site resources while those far from seminatural habitat used more on-site resources (Fig. 6). Unsurprisingly, bees nesting at riparian sites collected pollen primarily from seminatural habitats.

DISCUSSION

The role of landscape and local factors

The number of offspring produced by an animal living within a complex landscape is determined by characteristics of the habitat patch in which its nest is located, including the resources at the site, and by the distribution and abundance of resources over the wider landscape. In our system, the isolation of the nest site from seminatural habitat containing important food resources strongly affected the number of nests established and the number of offspring produced by the solitary bee *O. lignaria* (Table 1); however, this landscape level effect depended on the habitat type in which the nest was located (significant nesting habitat \times landscape interaction; Figs. 2 and 3). Previous studies of bees have shown that the amounts of different habitats surrounding focal sites (landscape composition) affect their diversity and abundance within mosaic agricultural

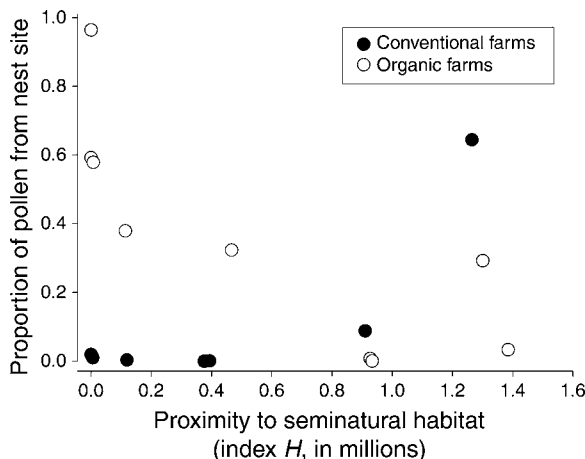


FIG. 6. Mean proportion of pollen collected from plants growing at the nest (i.e., on site and within the focal habitat type) as a function of isolation from seminatural habitat. More isolated sites are toward the origin. Index values (H) are calculated as in Fig. 2. Data are for bees nesting at conventional and organic farm sites.

landscapes (Kremen et al. 2002b, Steffan-Dewenter et al. 2002, Westphal et al. 2003). In those studies, as in our own, this landscape variable likely reflects in part the abundance and diversity of floral resources on which bee populations depend.

The pollen species used by *O. lignaria* and distributions of these flower species in the landscape revealed an important mechanism underlying the effect of isolation from seminatural habitat on offspring production and highlighted the importance of resources from different types of habitats to offspring production. Females used pollen from plants growing in multiple habitat types to provision their offspring, but they primarily collected resources from four native plant species growing in seminatural areas. Thus the amount of seminatural habitat in the surrounding landscape and its proximity to the nesting sites strongly affected reproductive output.

The landscape effect was most dramatic for bees nesting at conventional farms. Conventional farms within the agriculture-dominated matrix lacked native flowering plants and orchard crops, from which *O. lignaria* collects pollen (Torchio 1976), or such plants had finished flowering by the time adult *O. lignaria* emerged for the season. Instead bees relied on pollen from plants growing in remnant patches of riparian vegetation. These bees had to fly farther than did individuals nesting at riparian areas to collect resources for their offspring. The energy and extra time required to collect resources far from the nest would reduce the number of offspring produced of bees at these sites (Orians and Pearson 1979, Cresswell et al. 2000). Offspring production by females from conventional farms was strongly negatively correlated with distance to the nearest natural habitat ($r = -0.70$, $P = 0.05$). We

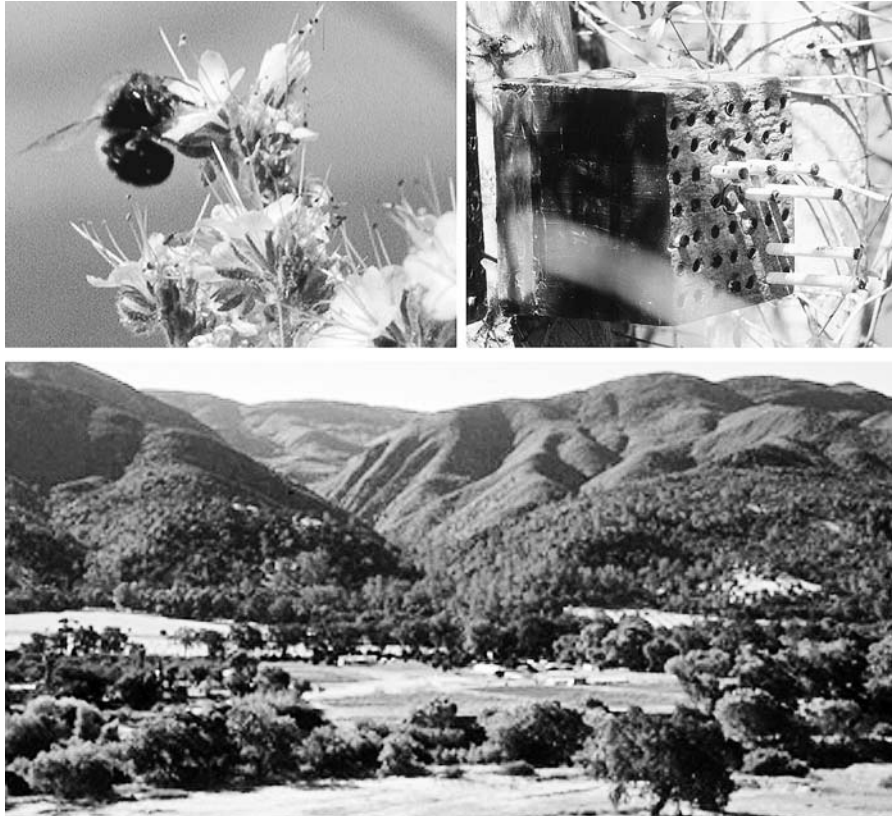


PLATE 1. (Top left) *Osmia lignaria* foraging on *Phacelia tanacetifolia* Benth. (Top right) An artificial nest block with paper straw inserts in which bees construct nests. (Bottom) Capay Valley, Yolo County, California, USA. A typical landscape surrounding NEAR sites in our study. The foreground is an agricultural mosaic landscape with chaparral and mixed-oak woodland behind. Photo credits: Top images N. M. Williams; bottom image, C. Kremens.

found no such correlation for bees nesting at organic farms ($r = 0.40$, $P = 0.22$) or riparian areas ($r = -0.22$, $P = 0.52$). The three conventional farms with the greatest proportion of natural habitat surrounding the nest site all had patches of flowering native plants on or directly adjacent to the farm. Bees at these sites had lower foraging costs and produced equivalent numbers of offspring compared to bees nesting on organic sites with similar degrees of isolation.

Bees nesting at organic farms were buffered to isolation from seminatural habitat by resources growing on the farm site. By collecting pollen from plants growing on site when seminatural habitats were too far away, females avoided travel to distant habitat patches to gather resources and so maintained consistent offspring production. Despite using on-site resources, bees at the more isolated organic farm sites still collected some pollen (9–62%) from beyond the farm itself (see Appendix). The shift between off-site and on-site foraging by bees at organic farms also explains the lack of correlation between local resource abundance and per capita offspring production.

Even bees nesting within remnants of riparian habitat used substantial amounts of pollen collected from other

types of natural habitat when available. Reproductive output by bees at FAR riparian sites nearly equaled that of bees on FAR organic sites (Fig. 3), and it increased with increasing natural habitat, exceeding that on NEAR organic farms (Figs. 2 and 3). The increase in offspring production with increasing natural habitat likely reflects the more abundant and diverse floral resources available in upland habitat adjacent to the riparian sites. Bees used *Salix* pollen from on site, but also used increasing proportions of *C. occidentalis* and *Lupinus* spp., which they most likely collected from adjacent upland areas (Fig. 4, Appendix). The decrease in use of *Salix* pollen with increasing proximity to natural habitat was seen for bees nesting in all habitat types and may reflect the decrease in the proportion of riparian habitat with increasing natural habitat overall. Alternatively *O. lignaria* may prefer *Cercis* pollen, and females may have collected more of it as it became available.

Theoretical and empirical studies have explored the importance of interpatch movement to population viability of a diversity of animals (Hanski and Gilpin 1997, Wolff et al. 1997, Hanski 1998, Hokit et al. 1999, Bergman and Landin 2002). Most efforts have focused on dispersal movements among similar types of habitats

within a “matrix” and on population dynamics over multiple generations rather than exploring within-generation movement. Connectivity among different types of habitat can also be important to both population persistence and ecological processes (Dunning et al. 1992, Ricketts et al. 2006; Talley et al. 2006). The diversity and abundance of bird, butterfly, and bee species sampled at single habitat locations all correlate with the diversity of habitats in the surrounding landscape, suggesting that access to different habitats promotes persistence even at individual sites (Weibull et al. 2000, Steffan-Dewenter et al. 2002). Observations of birds and bees show that individuals nesting in one habitat type forage in others (Osborne et al. 1999, Morris et al. 2001, Williams and Tepedino 2003). Although the temporal separation of central-place foraging and dispersal movements in bees differs from that of species that move through the landscape, such as butterflies (Schultz and Crone 2001, Sutcliffe et al. 2003), the importance of connectivity among habitats as identified for these taxa is likely to apply equally to bees.

Nest establishment, another key component of population persistence, paralleled the results for per capita offspring production in our study, suggesting that it, too, was affected by both local and landscape factors. The smaller numbers of nesting females at isolated conventional sites likely reflects limited resources available both on and off site. The lack of resources could increase prenesting mortality and would promote dispersal off site. Relatively higher nest establishment by females at isolated organic farms on which native plants were flowering, or on conventional farms near to natural habitat, suggests that the effect of habitat loss might be counteracted by restoring native plants at farm sites or conserving them within the landscape.

Osmia lignaria has a relatively short flight period during which few crop species bloomed. This timing no doubt promoted use of native plants over those flowering on farms. However, bee species whose flight seasons exceed the flowering period of individual plant species on which they rely may be equally likely to forage among habitat types as the resources they provide change during the season (Westphal et al. 2003).

Isolation and replacement value

The variation we observed in the reproductive success of bees among habitat types is likely to produce different population dynamics in intensively farmed landscapes compared to in those surrounded by natural habitat, with important consequences for persistence of bee populations. Females at all sites near to natural habitat produced enough offspring to replace themselves (Fig 3; site totals [mean \pm SE], conventional NEAR 35.3 \pm 13.5 offspring, organic NEAR 13.3 \pm 3.5, seminatural NEAR 90.0 \pm 45.9). Females at FAR conventional sites produced a total of 5.3 \pm 2.0 (mean \pm SE) offspring, far less than replacement for the 12 released (overall sex ratio 0.79 female : 1.0 male). These habitats

would be population sinks. At the isolated riparian patches and organic farms (FAR sites) reproductive output exceeded replacement (15.3 \pm 3.0, 27.1 \pm 6.2 offspring), and these might serve as source populations. These habitats represent a tiny fraction of the landscape. As a result, *Osmia lignaria* is likely to exist in small, isolated populations, vulnerable to local extinction. This process operating among multiple species of bees may explain the reduction in bee diversity and pollination services provided by native bees in some intensively farmed agricultural landscapes (Kremen and Chaplin, *in press*). To understand fully the spatial dynamics and long-term persistence of pollinator populations in such landscapes, future studies will also need to quantify dispersal among patches of natural habitat and farms in different landscape contexts.

Some researchers have suggested that bees, which rely on patches of resources that are commonly separated from nesting sites, may be buffered to the effects of fragmentation (Cane 2001). This characteristic may allow for important flexibility in how landscapes might be managed to promote the pollination of native plants and crops, although this flexibility is constrained by the foraging ranges of bees (Walther-Hellwig and Frankl 2000, Gathmann and Tschardt 2002). Our results suggest that options for conserving bees and the pollination services they provide within agricultural mosaic landscapes could range from small-scale “farm-scaping” that enhances habitat quality locally (e.g., some organic farms in this study) to landscape scale restoration and conservation of seminatural habitats that provide off-site resources within foraging ranges of the majority of bee species.

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APPENDIX

A table of pollens collected by *O. lignaria* at different sites within the agricultural–natural landscape (*Ecological Archives* A017-033-A1).