

Spatial and Temporal Heterogeneity of Pollen Foraging in *Osmia lignaria propinqua* (Hymenoptera: Megachilidae)

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ABSTRACT Pollen analysis from nest provisions of two populations of *Osmia lignaria propinqua* Cresson from the same valley over a 2-yr period showed a seasonal pattern beginning with willow, *Salix* spp. (Salicaceae), and progressing to bitter brush, *Purshia tridentata* (Rosaceae). Population I used twice as many pollen species but had similar niche breadths and constancy measures to Population II. There was a yearly difference in the percentage of the dominant pollens collected. The percentage of cells with one pollen showed between year, population, and season differences. There were no differences in the populations' nesting success or offspring production. The foraging differences apparently resulted from the proximity of the dominant pollens, *Salix* and *Purshia*, to the nest sites. *Salix* was a minimum of 600 m (one way) from Population I, but only 300 m from Population II. *Purshia* was within 200 m of both populations. The increased distance traveled by Population I bees allowed foraging on other pollen sources: *Camassia* (Liliaceae), *Ceanothus* (Rhamnaceae), *Delphinium* (Ranunculaceae), *Phacelia* (Hydrophyllaceae), and *Potentilla* (Rosaceae). These pollen species were available within 200 m but were rarely used by Population II. Bees were using as dominant pollen sources cornucopian species in the form of shrubs or small trees having showy floral displays of flowers with exposed, erect anthers extending beyond the petals.

KEY WORDS Insecta, *Osmia lignaria propinqua*, polylecty, pollen

BEES ARE CENTRAL-PLACE, patch foragers with larders of pollen-nectar that serve as food for offspring (Linsley 1958, Michener 1979). Detailed information on bee foraging is mostly limited to social species (Heinrich 1976, 1979; Inouye 1980; Seeley 1985; Seeley & Visscher 1988) or to extreme pollen specialists (Strickler 1979). Solitary bee species, the numerical majority (Linsley 1958, Michener 1979), have received only generalized treatment (Hurd 1979). Schemske's (1983) summary of Hurd (1979) for North American bees suggests that the majority of species (64.1%) show some degree of pollen preference either for species (15.3%), genus (36.6%), or family (12.2%) of flowering plants. Within the major bee families, these percentages vary with Andrenidae showing the greatest number of foraging specialists (83%) and Megachilidae the fewest (41.5%). Pollen preference, oligolecty, involves physiological, morphological, and behavioral adaptations to particular plant taxa (Linsley 1958; Linsley & MacSwain 1958; Thorp 1969, 1979; Cruden 1972; Eickwort & Ginsberg 1980). Individuals of specialist species will visit patches of the same resource and show similar foraging patterns. A broad pollen preference, polylecty, permits collection from a range of unrelated plants (Michener 1979). Generalist foraging can be complicated, however, by floral constancy, the strong individual preference for a particular pollen species (Grant 1950, Linsley 1958, Waser 1986) and local restriction in choice (Moldenke 1976, Fox & Morrow 1981). Individuals of generalist species foraging in

the same environment should encounter a variety of patches of favorable flowers and collect from them.

Osmia lignaria propinqua Cresson is a generalist forager that has been recorded visiting 46 genera in 24 families of flowering plants (Rust 1974, Hurd 1979), but locally it shows pollen preferences. Levin (1966) and Rust (1974) found almost exclusive use of *Hydrophyllum capitatum* Douglas in northern Utah. Torchio (1976; 1981a,b; 1985) found almost single species pollen foraging for bees released in apple, almond, pear, or prune orchards. Cripps & Rust (1989a,b) reported nine pollen species from scopal loads and nest provisions of bees from eastern Sierra Nevada Mountains in Nevada with *Phacelia*, *Salix*, and *Purshia* in greatest amounts. When offered a variety of flower species, bees released in a greenhouse (Rust 1974, Torchio 1989) or field cages (Phillips & Klostermeyer 1978) almost exclusively used *Phacelia tanacetifolia* Benth.

This paper addresses a fundamental question about polylectic species: Why do these regional polyleges show strong local preference for either a single or narrow group of species for their pollen? I compare the spatial and temporal pollen collecting patterns in two populations of *Osmia lignaria propinqua* from the same general area. These populations, controlled by nest site location, will encounter different patches of favorable flowers. However, local specialization or preference should result in the selection of similar dominant species. Seasonal changes in pollen phenology will result in

different pollens becoming available to the bee populations. Thus, pollen foraging specialization among individuals can be compared for temporal flexibility within and between populations, and between years.

Materials and Methods

The study site was Little Valley, approximately 27 km south-southwest of Reno, Nev. (Rust 1987). Within Little Valley, two sites were selected based on earlier nest collections of *O. lignaria propinqua* (Cripps & Rust 1985, 1989b; Rust 1987). The two sites were 1.6 km apart, and at the same elevation, 2,000 m. Site I was located in an approximately 1-ha dry meadow on the eastern edge of the valley. It was surrounded by pine forest and was approximately 200 to 300 m from the wet meadow that characterizes Little Valley. Nest Site II was also in a dry meadow, but the dry meadow merged within 50 m with the large wet meadow. At both sites, trap nests were placed within a 500-m² area on large (1+ m diameter) downed Jeffery pines, *Pinus jefferyi* Greville & Balfour, and their stumps. Dominant trees were Jeffery pine and lodgepole pine, *Pinus murrayana* Greville & Balfour, and the dominant shrub was bitter brush, *Purshia tridentata* (Pursh) de Candolle.

Trap nests (20 by 20 by 150 mm pine with single drilled holes of 5, 6, 7, and 8 mm diameter, and approximately 130 mm deep) were placed out in April and picked up in October. Two hundred and twenty-five nests were placed at Sites I and II in both years of the study. Nests were examined weekly and marked for nesting activity and time of completion. During the winter, nests were opened in the laboratory, and glycerine jelly pollen slides were made for each cell for pollen identification and determination of percentage by volume for the species present (Rust 1987, Cripps & Rust 1989b). Offspring survivorship was also recorded. A pollen reference collection was made from blooming species preserved in alcohol and prepared in a similar manner to the nest pollens. Most samples were identifiable to species, except for *Arctostaphylos*, *Ceanothus*, *Pinus*, *Potentilla*, and *Salix*, which were identified to genus.

Floral resource availability was measured weekly at both sites with two random 200-m transects radiating out from the trap nest sites. The second transect differed by $\pm 90^\circ$ from the first. At every other meter, a 0.5-m² quadrat was censused for blooming species and number of blossoms per species. Blossom is used for both single flowers and compound inflorescences of Asteraceae.

For Population I, *Salix* pollen was a minimum of 600 m (one way, straight line) from the trap nests, and bees had to negotiate 200 to 300 m of lodgepole pine forest before crossing the open wet meadow to the *Salix* bushes lining Franktown Creek. For Population II, *Salix* was 300 to 400 m from the nesting area and occupied an area of approximately 10 ha at the confluence of two forks

of Franktown Creek. For the two other pollen species collected but not present in the transects, *Arctostaphylos* shrubs were approximately 400 to 500 m from Population II and *Ceanothus* was approximately 300 m from Population I.

To calculate niche breadth, I used Levins (1968) normalized measure, $B_n = 1/R \sum p_i^2$, where p_i is the proportion, of all resource items used that consist of items in resource state i , i is a pollen species, and R is the number of available resource items or pollen species. R was determined by the number of pollen species found blooming in Little Valley that had appeared in the scopal loads (Cripps & Rust 1989b) or nest provisions (Rust 1987, Cripps & Rust 1989a) of *O. lignaria propinqua*. R did vary from week to week and year to year. For each sample interval, B_n is the mean of all nests completed during the interval.

The pollen species most abundant in the weekly cell samples was considered the dominant pollen collected.

Constancy was measured for each nest by comparing the overall percentage similarity (PS) (Southwood 1968) between the pollens in each adjacent cell beginning with the first constructed, $PS = (\sum_i (\min p_i \text{ in cell pair } i) / (n - 1))$. The adjacent cell PS values were summed and divided by $n - 1$ cells in the nest to produce the nest constancy. A nest with all cells having similar pollens will have a PS = 1.0, whereas a nest with all cells having different pollens, the PS = 0.0. For each sample interval, PS is the mean of all nests completed during the interval.

Because of a lack of completed nests during each week of the study, the weekly observations of floral resources and nesting activities were collapsed into three foraging periods: early (before 17 June 1983 and 26 May 1985), middle, and late (after 1 July 1983 and 10 June 1985). Each period represents an approximate 14-d interval for nesting, sufficient time to complete the cells per nest observed (Torchio 1989).

Data were analyzed with factorial analysis of variance (Ostle & Malone 1988) with pollen used being analyzed by four factors and interactions (year, population, season, and pollen species), and *Osmia* nesting and site floral resources by three factors and interactions (year, population or site, and season). All percentage data were arcsine transformed. The error term in these analyses was the three-way or the four-way interaction term and thus there was no test for heteroscedasticity (Ostle & Malone 1988).

Although *Pinus* pollen appeared in the provisions, it was not counted as an independently collected pollen because its appearance was from contamination of the blossoms visited by *O. lignaria propinqua* (Rust 1987). All pollens present including *Pinus* were included in niche breadth calculations and in pollen use factorial analysis of variance.

Table 1. Floral resources within 200 m of nesting sites of *O. lignaria propinqua* from Little Valley, Nev., during 1983 and 1985

Time	No. species	Mean no. blossoms/0.5 m ²	Dominant species ^a	No. quadrats with blossoms	Pollen species not present ^b
1983—Site I					
Early	10	2.8	Copa	56	Sa
Middle	17	8.6	Putr	78	Sa
Late	12	9.6	Phhu	66	Sa
1983—Site II					
Early	10	4.2	Copa	46	Sa, Ar
Middle	16	21.2	Phhu	74	Sa
Late	7	7.2	Pery	41	—
1985—Site I					
Early	19	2.5	Raal	42	Sa
Middle	23	18.4	Phhu	81	Sa, Ce
Late	28	10.3	Phhu	90	Sa
1985—Site II					
Early	16	3.2	Raal	59	Sa, Ar
Middle	19	17.6	Raal	86	Sa, Ar
Late	16	8.3	Pebo	78	Sa

^a Copa, *Collinsia parviflora*; Pery, *Penstemon rydbergi*; Pebo, *Perideridia bolanderi*; Phhu, *Phacelia humilis*; Putr, *Purshia tridentata*; Raal, *Ranunculus alismifolius*.

^b Ar, *Arctostaphylos* spp.; Ce, *Ceanothus* spp.; Sa, *Salix* spp.

Results

Flower Resources. Overall, the resource transects averaged 16.0 ± 5.8 (SD) ($n = 12$, range, 7–28) flowering species with 9.4 ± 6.4 blossoms per 0.5 m^2 ($n = 12$, range, 2.8–21.2) (Table 1). The number of species varied significantly between years ($MS = 200.08$; $F = 150.43$, $df = 1$, $P = 0.01$), sites ($MS = 52.08$; $F = 39.15$, $df = 1$, $P = 0.05$), and seasons ($MS = 25.33$; $F = 19.04$, $df = 2$, $P = 0.05$), while the mean blossoms present were similar between years, sites, and seasons, and interactions. *Collinsia parviflora* Douglas in 1983 and *Ranunculus alismifolius* (Gray) in 1985 were the numerically dominant early season flowering plants. Other season dominants varied between years and sites (Table 1) with four dominant species. Blossoms per quadrat differed significantly between years ($MS = 468.75$; $F = 20.99$, $df = 1$, $P = 0.05$) and seasons ($MS = 857.33$; $F = 38.39$, $df = 2$, $P = 0.05$) with approximately 33% ($n = 12$, range, 20–45) of the 200 quadrats measured per interval per site containing blossoms (Table 1). Pollen species absent from resource transects were *Salix* spp. from both sites, *Ceanothus* spp. from Site I, and *Arctostaphylos* spp. from Site II.

Nesting Biology. Cells per nest averaged 5.7 ± 2.1 ($n = 127$, range, 2.0–12.0) and there were no significant differences between years, sites, or seasons, or interactions in nest-cell production (Table 2). The 5.7 cells per nest is similar to other reports of *O. lignaria propinqua* nesting success (Rust 1974; Torchio 1985, 1989). The percentage of offspring surviving averaged $79.2 \pm 13.9\%$ ($n = 12$, range,

Table 2. Nesting biology of *O. lignaria propinqua*

Time	No. nests	Cells/nest	% Offspring survival
1983—Population I			
Early	37	5.37	89.9
Middle	30	5.20	89.7
Late	10	5.90	89.8
1983—Population II			
Early	10	7.50	82.6
Middle	4	5.25	76.1
Late	3	3.00	44.4
1985—Population I			
Early	4	6.25	84.0
Middle	10	6.90	86.9
Late	5	6.60	72.7
1985—Population II			
Early	4	6.50	88.4
Middle	8	6.00	85.4
Late	2	6.50	61.5

44.4–89.9), and there were no differences between years, sites, or seasons, or interactions in the percentage of cells producing viable offspring (Table 2).

Pollen Foraging. The number of pollen species available to both populations was the same (Table 3). The average number used was 2.2 ± 0.92 ($n = 127$, range, 1–6). However, the trend in species used differed over seasons ($MS = 3.250$; $F = 39.157$, $df = 2$, $P = 0.05$), populations ($MS = 24.080$; $F = 290.12$, $df = 1$, $P = 0.01$), and there were also significant year \times season interaction ($MS = 2.250$; $F = 27.108$, $df = 2$, $P = 0.05$) and population \times season interaction ($MS = 5.08$; $F = 61.205$, $df = 2$, $P = 0.05$). Population I used approximately twice (6.0 ± 1.5 , $n = 6$, range, 4–8) as many pollen species as Population II (2.8 ± 0.7 , $n = 6$, range, 2–4) (Table 3). Only once (Population I, middle season 1985) were all available eight pollen species used by the bees. Mean number of species used showed only a significant population difference ($MS = 1.449$; $F = 55.099$, $df = 1$, $P = 0.05$) with Population I again using on average more species (Table 3). The bees showed a selection for certain pollen species from those available (Fig. 1; Table 4). Factorial analysis of variance testing showed significant pollen species ($MS = 2,789.6$; $F = 70.422$, $df = 9$, $P = 0.01$), pollen species \times year interaction ($MS = 303.6$; $F = 7.666$, $df = 9$, $P = 0.01$), pollen species \times population interaction ($MS = 225.9$; $F = 5.705$, $df = 9$, $P = 0.01$), pollen species \times season interaction ($MS = 278.8$; $F = 7.039$, $df = 9$, $P = 0.01$), pollen species \times population \times year interaction ($MS = 137.9$; $F = 3.482$, $df = 9$, $P = 0.05$), and the pollen species \times population \times season interaction ($MS = 163.5$; $F = 4.128$, $df = 18$, $P = 0.01$) with pollens used by *O. lignaria propinqua* bees. The dominant pollens used were *Salix* spp. and *Purshia tridentata* (Fig. 1; Tables 3 and 4). *S. lemmonii* Bebb was the first collected pollen by both populations and in

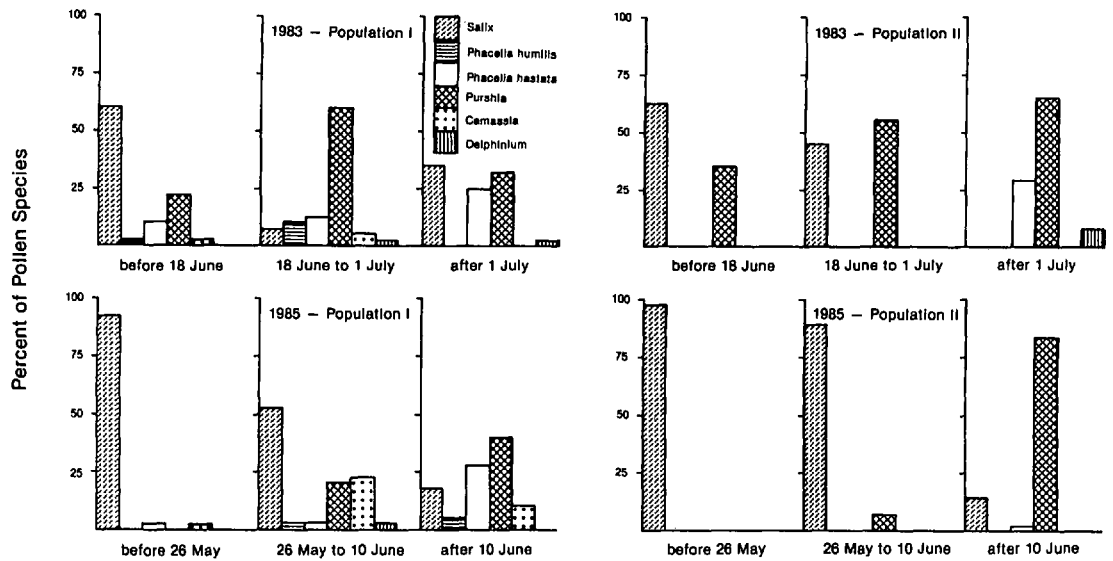


Fig. 1. Percentage of major pollens collected during the three foraging periods by two populations of *O. lignaria propinqua* from Little Valley, Nev., during 1983 and 1985. Percentages of all pollens collected are given in Table 4.

both years. This was followed by *Purshia* in 1983, but remained *Salix* in 1985. Late-season foraging in 1983 showed Population I returning to *Salix lasiolepis* Benth., whereas Population II continued to use *Purshia*. In 1985, both populations switched to *Purshia* late in the season (Fig. 1; Table 4). Once (Population I, middle season 1983) *Purshia* was the transect and foraging dominant pollen.

There was a significant yearly difference in the percentage of dominant pollen ($MS = 742.1$; $F =$

19.193, $df = 1$, $P = 0.05$) with 1985 provisions averaging $77.2 \pm 24.4\%$ ($n = 6$, range, 40.6–99.2) dominant pollen and 1983 provisions averaging $56.5 \pm 9.8\%$ ($n = 6$, range, 37.9–64.6) (Table 3). Niche breadths averaged 0.237 ± 0.103 ($n = 127$, range, 0.125–0.835) and showed no significant differences (Table 3). The percentage of cells with a single pollen averaged 0.45 ± 0.39 ($n = 127$, range, 0.0–1.0) and showed significant interactions between all pairs of factors ($years-MS = 680.1$; $F = 162.706$,

Table 3. Pollen analysis from cell provisions of *O. lignaria propinqua*

Time	No. species available	No. species used	Mean no. species used	% Dominant pollen ^a	Niche breadth B_n	% Cells with 1 pollen	Constancy PS
1983—Population I							
Early	8	7	2.05	Sa, 58.8	0.204	61.3	0.86
Middle	8	7 ^b	2.73	Putr, 61.3	0.247	12.1	0.87
Late	7	4 ^b	2.10	Sa, 37.9	0.283	49.1	0.92
1983—Population II							
Early	8	4	2.00	Sa, 62.6	0.206	54.6	0.91
Middle	8	2 ^b	1.75	Putr, 54.2	0.217	28.5	0.89
Late	7	3	1.66	Putr, 64.6	0.256	44.4	0.93
1985—Population I							
Early	6	5	2.00	Sa, 93.7	0.235	84.0	0.96
Middle	8	8 ^b	3.20	Sa, 52.5	0.303	40.5	0.71
Late	7	5	3.00	Putr, 40.6	0.416	27.2	0.76
1985—Population II							
Early	6	2	1.25	Sa, 99.2	0.203	96.1	0.99
Middle	8	3	1.75	Sa, 91.5	0.151	79.1	0.92
Late	7	3	2.50	Putr, 86.0	0.264	38.4	0.87

^a Putr, *Purshia tridentata*; Sa, *Salix* spp.

^b *Pinus* pollen present in provisions.

Table 4. Percentage of the pollen species appearing in the provisions of *O. lignaria propinqua*

Date	Pollen species ^a									
	Sa	Ar	Po	Phhu	Phha	Putr	Caqu	Denu	Ce	Pi
1983—Population I										
Early	58.8	1.5	1.0	2.3	10.7	23.3	2.4	—	—	—
Middle	7.3	0.6	—	8.3	11.5	61.3	6.4	3.7	—	0.9
Late	37.9	—	—	—	25.4	33.7	—	2.0	—	1.0
1983—Population II										
Early	62.6	1.8	—	0.2	—	35.4	—	—	—	—
Middle	44.0	—	—	—	—	54.2	—	—	—	—
Late	—	—	—	—	28.6	64.6	—	6.8	—	—
1985—Population I										
Early	93.7	3.3	—	—	1.6	—	1.2	0.2	—	—
Middle	52.5	0.8	—	0.6	1.7	20.1	23.1	0.3	0.6	0.3
Late	18.0	—	—	4.2	27.0	40.6	10.2	—	—	—
1985—Population II										
Early	99.2	0.8	—	—	—	—	—	—	—	—
Middle	91.5	1.3	—	—	—	7.2	—	—	—	—
Late	13.0	—	—	—	1.0	86.0	—	—	—	—

^a Ar, *Arctostaphylos* spp.; Caqu, *Camassia quamash*; Ce, *Ceanothus* spp.; Denu, *Delphinium nuttallianum*; Phha, *Phacelia hastata*; Phhu, *P. humilis*; Pi, *Pinus* spp.; Po, *Potentilla* spp.; Putr, *Purshia tridentata*; and Sa, *Salix* spp.

df = 1, $P = 0.01$; populations—MS = 118.4; $F = 28.335$, df = 1, $P = 0.05$; seasons—MS = 737.7; $F = 176.483$, df = 2, $P = 0.01$; year \times population—MS = 193.6; $F = 46.316$, df = 1, $P = 0.05$; year \times seasons—MS = 244.3; $F = 58.467$, df = 2, $P = 0.05$; population \times seasons—MS = 115.1; $F = 27.548$, df = 2, $P = 0.05$). More cells early in the nesting season had a single pollen ($86.2 \pm 3.4\%$ *Salix lemmonii*, $n = 4$, range, 58.8–99.2), and the percentage declined seasonally in 1985 but showed a slight late-season increase in 1983 (Table 3). Percentage of similarity, constancy, averaged 0.87 ± 0.15 ($n = 127$, range, 0.2–1.0) and showed no significant differences between years, sites, or among seasons.

Discussion

Both populations of *O. lignaria propinqua* were using the same species for the majority of the pollen in cell provision formation, *Salix* spp. and *Purshia tridentata*. Both populations showed similarities between years, sites, and among seasons for niche breadths and foraging constancy and between sites, and among seasons for the percentage of the dominant pollen collected. However, bees in Population I visited significantly more species. Why with both populations showing the majority of their foraging on two cornucopian species (Mosquin 1971) should one population visit so many additional species? Floral resource data provide little or no information other than the absence of *Salix* spp. from the immediate vicinity of both nesting sites.

Both populations visited *Salix* spp. early in the nesting season. During the middle and late parts of the nesting season, *Purshia* pollen became available at both nesting sites and throughout Little Valley, and Population II bees switched to this second cornucopian species. Population I, however, showed a combined use of *Salix* spp. and *Purshia* with substantial use of *Phacelia hastata* (25%). The significant two-way interactions (year \times species and population \times species) in the species used by *O. lignaria propinqua* support these foraging differences. There were differences in the species used over the season, but they were not consistent between years or between populations. This same pattern was observed and statistically supported with the percentage of cells with a single pollen (Table 3). There were differences in the percentage of cells with one pollen, but they were not consistent between years, populations, or seasons.

Bees from Population I flew approximately 1.2 km to provision with *Salix* pollen. This distance most likely explains the collection of *Camassia* and *Delphinium* pollen by these bees as they crossed the wet meadow to obtain *Salix* pollen. These two pollens were essentially absent from the pollen provisions of Population II bees although both were present within 200 m. The extended foraging flights of Population I bees probably brought them in contact with *Ceanothus* and *Potentilla*. It is interesting to note that *Potentilla* plants occurred be-

tween the nesting site and the wet meadow, but *Ceanothus* shrubs were located in the opposite direction away from the wet meadow.

The economics of central-place foraging (Schoener 1979, Orians & Pearson 1979) predicts that foragers should stay longer on and return with heavier resource loads from more distant, rich resources. Thus, *Salix* spp. is a rich resource for *O. lignaria propinqua* and thus they are persistent in collecting its pollen. Population I bees were on average traveling twice as far as Population II bees for *Salix* pollen but their nesting rate per female and offspring survival was the same as Population II. The interpretation here is that something other than flight distance to and from abundant resources must limit reproductive output of *O. lignaria propinqua*.

The differences in the number of species in bloom and the 3-wk difference in nesting between 1983 and 1985 resulted from the extremely heavy snow pack of the 1982–1983 winter versus the near normal winter precipitation of 1984–1985 (James 1984). The heavy snow pack produced a delay in snow release and greatly altered plant phenologies (Nachlinger 1985). Snow pack data are not available for Little Valley, but two close, similar-elevation U.S. Weather Stations (Boca, Nevada County, Calif., 39°22'N–120°6'W, elevation 1,699 m, and Glenbrook, Douglas County, Nev., 39°5'N–119°57'W, elevation 1,935 m) recorded 107.0 and 83.6 cm precipitation between September and April in 1982–1983, respectively, and 38.3 and 30.4 cm in 1984–1985, respectively (USDC-NOAA 1982–1985a,b).

Local foraging specialization by *O. lignaria propinqua* is also reflected by the percentage of cells containing only one pollen and the high constancy measure. These specialization patterns recorded from natural sites are very similar to those obtained when *O. lignaria propinqua* was released in apple (*Malus sylvestris* P. Miller), prune (*Prunus* spp.) (Torchio 1976), or almond (*Prunus americana* L.) orchards (Torchio 1981b). These released populations averaged 79% apple and prune pollen and 96% almond pollen, respectively. For bees released in apple and prune orchards, two other pollens were collected, currant (*Ribes* sp.) and dandelion (*Taraxacum officinale* Wiggers). Few cells had a preponderance of those pollens. In almond orchards, the other 4% pollen was an unidentified crucifer pollen. Eighty-five percent of the cells contained only almond pollen.

Raw (1974) found that *Osmia rufa* (L.) collected from 38 to 71% *Ranunculus* pollen from four sites in England. At three sites, the other dominant pollen was *Quercus* (Fagaceae) and *Rubus* (Rosaceae) at the fourth. These pollens represented >90% of the pollens collected by *O. rufa*. Tasei (1976) recorded that *Osmia coerulescens* L. collected pollen from 30 plant species in 10 families in west central France. First-generation bees collected 66% Fabaceae (10 genera) and 31% Lamiaceae (11 genera)

pollen, while second-generation bees collected from 8 families. The pollen foraging patterns were fairly constant over a 4-yr period. These two species are generalists that like *O. lignaria propinqua* show local specialization on particular floral types.

Seven of the nine flowering plants visited by *O. lignaria propinqua* in Little Valley, although in five families, had similar flower structure. *Salix* spp. (Salicaceae), *Phacelia hastata* Douglas & Lehmann, and *Phacelia humilis* Torrey & Gray (Hydrophyllaceae), *Potentilla* spp. and *Purshia tridentata* (Rosaceae), *Ceanothus* spp. (Rhamnaceae), and *Camassia quamash* (Pursh) Greene (Liliaceae) all have open flowers with exposed, erect stamens (Munz & Keck 1965). Stamen filaments are as long as or longer than the petals thus placing the anthers beyond them. *O. lignaria propinqua* collects pollen by drawing the anthers to the scopal hairs with the hind legs (Cripps & Rust 1989a). The opposite is found in the other two species visited, *Arctostaphylos* spp. have small urn-shaped flowers with included stamens and *Delphinium nuttallianum* Pritzl has irregular flowers with included stamens. Both of these species have flowers that produce much concealed nectar and may represent the nectar source for longer foraging flights to *Salix*.

Nectar is required in provision formation (Krombein 1967; Rust 1974; Torchio 1985, 1989). If *Arctostaphylos* and *Delphinium* are nectar sources used in provision formation when pollen sources are without or with limited nectar, then some of the pollen grains present may be from contamination while the bee collects nectar. *Arctostaphylos* pollen averaged $1.4 \pm 0.9\%$ ($n = 12$, range, 0.6–3.3) and *Delphinium* averaged $2.6 \pm 2.7\%$ (range, 0.2–6.8). *Arctostaphylos* and *Delphinium* pollen percentages are below the 3.0% *Pinus* pollen appearing in *Osmia* provisions as contamination (Rust 1987) and can be considered the same. *Delphinium* pollen percentage approaches 3.0% and may be collected while the bee obtains nectar from the petal spurs. Twenty-one of the 46 genera of flowering plants listed by Hurd (1979) have flowers with exposed stamens and most likely represent pollen sources for the bee. The remaining 25 genera have flowers with included stamens and may be regarded as nectar sources.

One question still remains: Why are *Salix* and *Purshia* the dominant pollen species for *O. lignaria propinqua* in Little Valley and not the other species with exposed, erect stamens? *Salix* and *Purshia* are medium-sized shrubs to small trees, locally very abundant, and during flowering they have impressive floral displays; they are cornucopian species (Mosquin 1971). Apple, prune, and almond also fit this pattern. *Ceanothus* fits this description but has smaller flowers, perhaps making pollen collecting more difficult.

The four remaining pollen sources are forbs. *Camassia* and *Phacelia* have long, erect filaments placing the anther well beyond the sepals and petals. *Potentilla* has the shortest filaments, perhaps

making pollen collecting more difficult. *Hydrophyllum* (Levin 1966, Rust 1974) and the greenhouse pollen plant, *Phacelia tanacetifolia* (Phillips & Klostermeyer 1978, Torchio 1989), are forbs with long, erect filaments exposing the anthers. Thus pollen-foraging behavior and flower design characterize pollen sources for *O. lignaria propinqua* that includes genera in many families of flowering plants. Bees respond locally to the species presenting the correct flower configuration and most abundant pollen.

Levin & Haydak (1957) provide information that *O. lignaria propinqua* has a developmental response to particular pollens and that other pollens reduce or even prevent larval development. Larvae reared on *Hydrophyllum capitatum*, the natural pollen, grew larger and faster than larvae reared on pea (*Pisum sativum* L.), alfalfa (*Medicago sativa* L.), or mustard (*Brassica nigra* L.) pollen. Larvae reared on gumweed (*Grindelia spuarrosa* (Pursh)) povertyweed (*Iva axillaris* Pursh) and dandelion died before reaching the final instar. I recorded 53% larval mortality (8 of 15 cells) in cells provisioned with dandelion pollen when the apple bloom failed and bees were still actively nesting (unpublished data).

The pollen-foraging pattern described for *O. lignaria propinqua* does not change the interpretation of polylecty and oligolecty. By definition (Linsley & MacSwain 1958, Michener 1979), *O. lignaria propinqua* is polylectic, collecting from unrelated plant families. However, these unrelated pollen sources appear to have several common features: flowers with multiple, exposed, erect stamens on long filaments and usually shrub or small tree form. These characteristics define an *Osmia lignaria propinqua* floral syndrome. Thus, regionally this species is polylectic, but with strong local preferences for a single source or narrow group of structurally similar plants.

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