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Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*

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Female bees are usually confronted with a choice among several flower species that differ in their location and abundance within the community, and in the efficiency with which their pollen and nectar can be harvested. We investigated the effects of distance and flower density of two flower species on pollen collection by providing nest locations for the mason bee *Osmia lignaria* in natural settings. Distance weakly affected pollen use; on average, bees nesting near a flower species tended to collect more of its pollen than did bees nesting at a greater distance. Flower density did not predictably impact pollen use, and use did not track changes in density during the season. Bees consistently mixed pollen from more distant species, despite substantial added foraging costs, and also mixed when one species was an order of magnitude less abundant than the other. Bees require nectar as well as pollen to feed their offspring, and our preliminary data suggest that the efficiencies of pollen and nectar collection are inversely related between the two flower species, which would favor visitation to both species. Bees appear to collect some pollen from the low-pollen, high-nectar plant while visiting it for nectar. Thus, a nectar-collecting constraint may favor collecting pollen from mixtures of species. *Key words:* central place foraging, complementary nutrients, nectar, *Osmia*, pollen, resource abundance, solitary bee, spatial distribution. *[Behav Ecol 14:141–149 (2003)]*

Many animal foragers consume, cache, or feed resources to offspring at a central location or nest (Dearing, 1996; Fryxell and Doucet, 1991; Schmid-Hempel et al., 1985; Ydenberg, 1994). The time and energy costs incurred as foragers travel between the resource patches and central place help determine foraging profitability and may affect inclusion of particular patches, and different resource species within them. Because foraging costs are thought to be directly influenced by the distance from the nest to resource patches, foragers should minimize the distances they travel (Frey-Roos et al., 1995; Fryxell and Doucet, 1991; Orians and Pearson, 1979).

Also potentially affecting the diversity of the diet for central place foragers are density and composition of resources within patches. Such choices are simplified in cases in which resource species are segregated into separate monospecific patches (e.g., fruiting or flowering shrubs and trees; Davidar and Morton, 1986; Frankie et al., 1976), because diet choice becomes synonymous with patch choice and is determined by the density of the signature resource and the rate at which it may be exploited. When patches are monospecific, we expect the energy-determined diet to be less diverse because mixing incurs additional between-patch travel costs.

Bees are among the few insect taxa that can be categorized as central place foragers. Females of most species collect pollen and nectar and mold them into separate provisions for each offspring in the nest. The effects of the distance to, and density of, pollen and nectar plants on foraging by bees are poorly known. Workers of some social species alter the size of nectar loads and visitation rates as a function of distance to nectar resources (Bartareau, 1996; Kacelnik et al., 1986; Núñez, 1982; Schmid-Hempel, 1987). Only one study has directly addressed the effect of density on pollen foraging (Rasheed and Harder, 1997), and another hypothesized that females of one solitary bee species, *Osmia lignaria*, increased the diversity of pollen species collected when the preferred pollen species grew farther from the nest (Rust, 1990).

Optimizing rates of energy gain are not the only alimentary challenges that foraging animals face. For many animals, especially herbivores, the distribution of essential nutrients and toxins varies among plant species (Bernays et al., 1994; DeMott, 1998; Slansky, 1992). When essential nutrients are inadequate within an otherwise profitable species, a forager must add alternates, even if it is energetically expensive to do so (Belovsky, 1978; Doucet and Fryxell, 1993; Pennings et al., 1993; Pulliam, 1975; Rapport, 1980; Westoby, 1978).

Female bees face a related problem. They make repeated foraging trips from their nests to collect two categories of nutrients, pollen and nectar. These foodstuffs are high in protein and carbohydrates, respectively (Baker and Baker, 1983; Roulston et al., 2000), and are essential for larval development and adult nutrition. In social species, the subjects of most studies of foraging in bees, it is easy to divorce pollen and nectar foraging because individual workers often specialize on one or the other resource. In solitary species, each female must collect all pollen and nectar herself, and in species that do not remix the final provision mass (e.g., *Osmia lignaira*; Torchio, 1989), they must collect both resources on most foraging trips. Thus, these females may be forced to balance the efficiency of both pollen and nectar collection (Tepedino and Parker, 1982; Thomson, 1988).

Within this context, we address the effects of distance from the nest to, and availability of, pollen and nectar on pollen use in the bee *Osmia lignaria*. Williams (1999) has shown that female *O. lignaria* nearly always collected mixtures of two native pollen and nectar resources, *Hydrophyllum capitatum* (Hydrophyllaceae) and *Salix* spp. (Salicaceae), when they were spatially intermingled and presented in equal abundance. In natural communities, these species often grow in discrete

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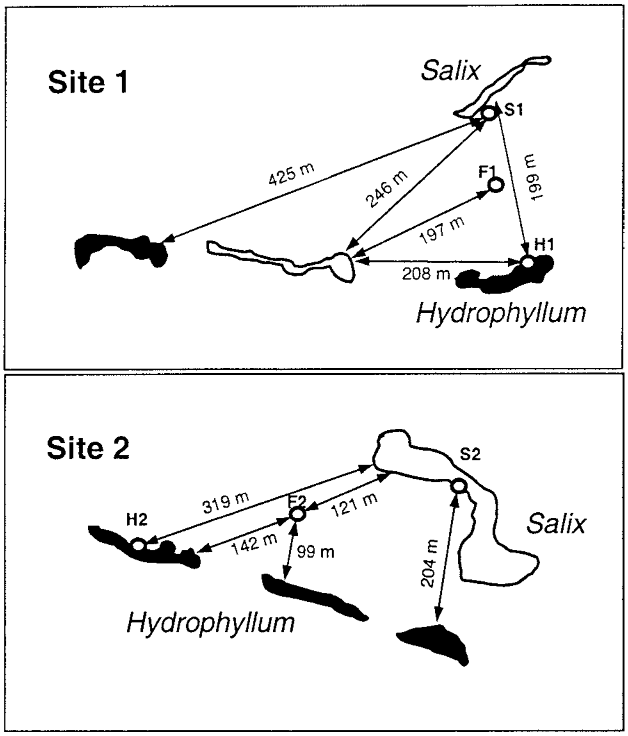

Figure 1
Research sites, with distances from nest locations (circles) to each resource species. Dark-shaded patches contained *Hydrophyllum capitatum,* and light-shaded patches contained *Salix* spp.

patches separated by tens to hundreds of meters, *Salix* most commonly in riparian areas and *H. capitatum* at woodland edges (Shaw, 1989). *Osmia lignaria* females nest in both habitats and are therefore commonly located near one species and distant from the other.

We propose four hypotheses concerning pollen collection in populations in which alternative resources grow in distinct patches: (1) bees collect more pollen from sources nearest the nest; (2) a bee's collection of a resource is positively related to the density of that resource; 3) bees nesting within patches of spatially separated resources construct fewer mixed provisions than those nesting intermediate to the two resources; and (4) during individual foraging trips bees visit primarily a single resource patch.

METHODS

The system

The bee species

In northern Utah, *Osmia lignaria propinqua* emerge beginning in late April, coincident with the flowering of spring ephemeral herbs and shrubs (Cripps and Rust, 1989). Females construct a linear series of brood cells within naturally occurring tunnels or cracks in wood (Levin, 1966; Rust, 1974). Each cell contains an egg atop a provision of pollen and nectar. Females readily accept as nests tunnels drilled into twigs or wood blocks, lined with paper drinking straws, and attached to trees or shaded posts. Straws can be removed while females are absent and held to the light to reveal the progression of nest construction.

Dry weights (± SE) of *O. lignaria* provisions range from 0.135 ± 0.001 g (male offspring) to 0.243 ± 0.003 g (female offspring) and contain 53.3–56.0% pollen by volume (Bosch J and Kemp W, unpublished data; Williams NM, unpublished data). Females make between 14–35 pollen-nectar trips per provision and carry between 3.4×10^6–3.9×10^6 pollen grains and ~13 µl of nectar per trip (Torchio, 1989; Williams, 1999). The number of inflorescence visits required to gather a full load of pollen and nectar depends strongly on the plant species visited and standing crops of each resource. In flight-cages containing mixtures of *Salix* and *H. capitatum* flowers, females visited 24.13 ± 1.47 inflorescences per trip (n = 46 trips by 11 females; Williams NM, unpublished data).

Flower species

Provisions from nests sampled in the Cache Valley, Cache County, Utah, contain predominantly pollen of *Salix* species (Salicaceae), *H. capitatum (*Hydrophyllaceae), and several shrubs (Rosaceae, Berberidaeceae; Williams, 1999). Three *Salix* species (*S. exigua, S. lasiandra,* and some *S. fragilis*) bloomed together within the same discrete stands during the nesting period (6–21 May 1997); because all three were visited for pollen and nectar during single foraging trips in field and greenhouse studies (Williams, 1999), we treat them as a single *Salix* resource throughout. Abundant *H. capitatum* also grew in discrete patches separated from *Salix* by intervening old fields that contained no common flowers of any species during the study period.

Study design

To examine the effects of resource proximity on pollen use, we provided nest locations of *O. lignaria* in the lower reaches of two canyons that open into Cache Valley, Cache County, Utah. Throughout the season, we monitored flower densities and pollen use at each site. Both sites included boundaries of woodland and old-field, and riparian areas. At each site, we placed wood nesting-blocks at each of three locations: the edge of a *Salix* patch (S1 or S2, sites 1 and 2 respectively; Figure 1), the edge of an *H. capitatum* patch (H1 or H2), and the middle of the field between the two resource patches (F1 or F2). Site and block positions were chosen so that the nests at H1 and H2 locations were farthest from *Salix* bloom, and nests at S1 and S2 locations were farthest from *H. capitatum* bloom. We mapped resource patches and nest locations by using a Landmark System GPS (Juniper Systems, Logan, Utah, USA). Averaged from the center of flower patches, S1 and S2 nest locations were 340.0 and 257.1 m from *H. capitatum,* and H1 and H2 nests were 247.4 and 358.9 m from *Salix.* Site 1 contained two distinct patches of each *Salix* and *Hydrophyllum,* and the averages reflect both patches.

Monitoring nesting and resources

At each site, we monitored nesting and floral resources every third day from the onset of nesting on 6–21 May, when both plant species finished blooming. On each monitoring day, we scored the number of completed and active nests per nest location and marked the progress of active nests within each straw. These marks enabled us to assign exact dates to provision construction and calculate the number of cells constructed during the 3-day period. Filled straws were moved to a cold room in the laboratory to preserve pollen for sampling. These straws were replaced with empties so that bees always had vacant holes available. We scored the number of open *Salix* and *H. capitatum* inflorescences in twenty 2.0 × 0.5-m quadrats, spaced at 10-m intervals along transects within the patches of each plant species. Only inflorescences that contained freshly open flowers were included. Male and female *Salix* clones grew interspersed in the patches.

For each species we also counted the number of flowers open on 10 inflorescences each day. We counted the number of pollen grains available in unvisited flowers (*H. capitatum*, $n = 40$) and inflorescences (*Salix*, $n = 10$) of each species. Pollen counts were made using an Elzone 280 particle counter (Micromeritics Inc., Atlanta, Georgia, USA).

Assessing pollen species delivered

We sampled pollen from a randomly selected set of 15 brood cells completed on each date that resources were assessed. On early dates when fewer than 15 bees were nesting, we sampled fewer cells. Each sample came from a different nest. We stained a minute sample of pollen from the middle of each provision with basic fuchsin in glycerin jelly (Beattie, 1971) and identified pollen species using a compound microscope. Pollen use for each species is reported as the proportion of the total number of pollen grains of all species counted in that provision (300 grains). A preliminary analysis showed that although proportions of each species differed among samples from front, middle, and rear parts of a provision, within-site comparisons of pollen use among nesting locations did not differ whether single or pooled samples from the three positions were used. We therefore used single samples for these comparisons.

For some analyses, we were interested in the number of provisions that contained pollen from a single species (pure provisions) versus mixtures from two or more (mixed provisions). Provisions may contain trace amounts of pollen not actively collected because nectar-foraging bees will pick up some pollen incidentally. Thus, we scored provisions containing greater than 95% of one pollen species as pure and others as mixed.

Within-trip pollen mixing

Mixed-pollen provisions can result from separate trips to each plant species or a series of mixed trips. To distinguish these behaviors, we removed three samples from different positions within the same provision for a set of 98 provisions collected on three dates at Site 2. Because *O. lignaria* females mix only the top layer of pollen on the growing provision between foraging trips and do not remix the entire provision before oviposition (Torchio, 1989), a sample taken from a single point within the provision provides an estimate of the proportions of pollen collected within a single foraging trip. Samples from within the same provision that contain single, but different, species of pollen would indicate separate trips to each plant species rather than mixed-pollen trips.

Analyses

We used general linear models to test the effects of distance from a bee's nest to patches of alternative flower species and density of each flower species on the proportion of pollen collected from each species. We included nest location (distance) as categorical variable and the flower density for each species as continuous variables (SAS/STAT Proc Mixed; SAS, 1998). We used paired *t* tests to compare nest locations, following a significant overall effect. Pollen samples from the same location are not truly independent measures, we therefore used the mean proportion of each pollen species at each location date (based on 15 samples) as variates for our analysis. Proportion-pollen was arc-sine transformed to normalize the data. The variances among locations remained heterogeneous for *H. capitatum* so we used heterogeneous variance models for analyses. The magnitude of the distance effect and the interaction with resource density differed between sites, and we therefore report separate analyses for each site to clarify interpretation.

Because the proportions of the pollen species must sum to 1.0, these response variables lack statistical independence (Aitchison, 1986; Jackson, 1997). We addressed this issue in two ways. First, because our interest was primarily in *Salix* and *H. capitatum* use, we performed univariate tests for *Salix* and *H. capitatum.* Second, when *Crataegus douglasii* unexpectedly appeared as a significant pollen component on some dates, we excluded it from the analysis by taxa, but we still calculated proportional *Salix* and *H. capitatum* use by including the *C. douglasii* component in the denominator. Excluding it entirely would have changed the estimated proportions of *Salix* and *H. capitatum* used and misrepresented foraging of the bees (Johnson, 1980). This protocol helped provide greater statistical independence between the *Salix* and *H. capitatum* components (for a similar approach, see Latta and Linhart, 1997). *Crataegus* pollen unexpectedly formed a substantial portion of many provisions, and we lacked data on its abundance. Thus, we decided that the loss of information on the *Crataegus* component was worth the increased statistical independence. At Site 1, variables were not correlated after removing the *Crataegus* component. At Site 2, proportional *H. capitatum* and *Salix* use remained correlated at all nest areas (H2: Kendall $\tau = -0.568$, $p < .001$; F2: $\tau = -0.641$, $p < .001$; S2: $\tau = -0.895$, $p < .001$). We report separate values for *Salix* and *H. capitatum* for both sites, but we recognize that for Site 2, the two do not represent fully independent results.

We explored brood-cell production as a function of inflorescence density and nest location by using a general linear model similar to that for pollen collection. The initial model showed no significant interaction between the effects of density of each plant species, so we used total inflorescence density of the two species in our final analysis.

We compared the proportion of mixed provisions constructed by females between sites and nesting locations by using logit models (Proc Genmod, SAS/STAT; SAS, 1998). Differences among locations within sites were tested by using contrast statements with significance levels adjusted for multiple comparisons (Sokal and Rohlf, 1995).

RESULTS

Resource characteristics

The two sites were similar in floral phenology (onset and cessation of bloom and its pattern of production, Figure 2); and relative abundance of the two plant species, although the ratio of total *Salix* to *H. capitatum* inflorescences was much greater at Site 2 than at Site 1 (Figure 2C,D). In addition to the focal species, several *C. douglasii* trees bloomed during the first half of the season at Site 2 and throughout the season at Site 1 (exact timing of bloom not established).

Distance to resources

The distance from bee nests to each flower species affected pollen collection; however, the distance effect differed between pollen species and sites (Table 1). On average, bees nesting near a given species tended to collect more of its pollen relative to bees nesting farther away (Figures 3 and 4). At Site 1, bees nesting within *Salix* patches (S1) collected significantly more *Salix* pollen than bees nesting within *H. capitatum* patches (H1, Figure 3A; $t = 6.05$, $df = 3.03$, $p_{adj} = .02$, Tukey-Kramer adjusted); however, bees nesting at H1 did not collect significantly more *H. capitatum* pollen than did bees at S1 (Figure 3B; $t = 1.16$, $df = 2.09$, $P_{adj} = 0.37$). The lack of a significant distance effect on *H. capitatum* collection was likely due in part to an influence of *C. douglasii* pollen, which bees appear to have collected instead of *H. capitatum* during the first part of the season (Figure 3B,C). Separate

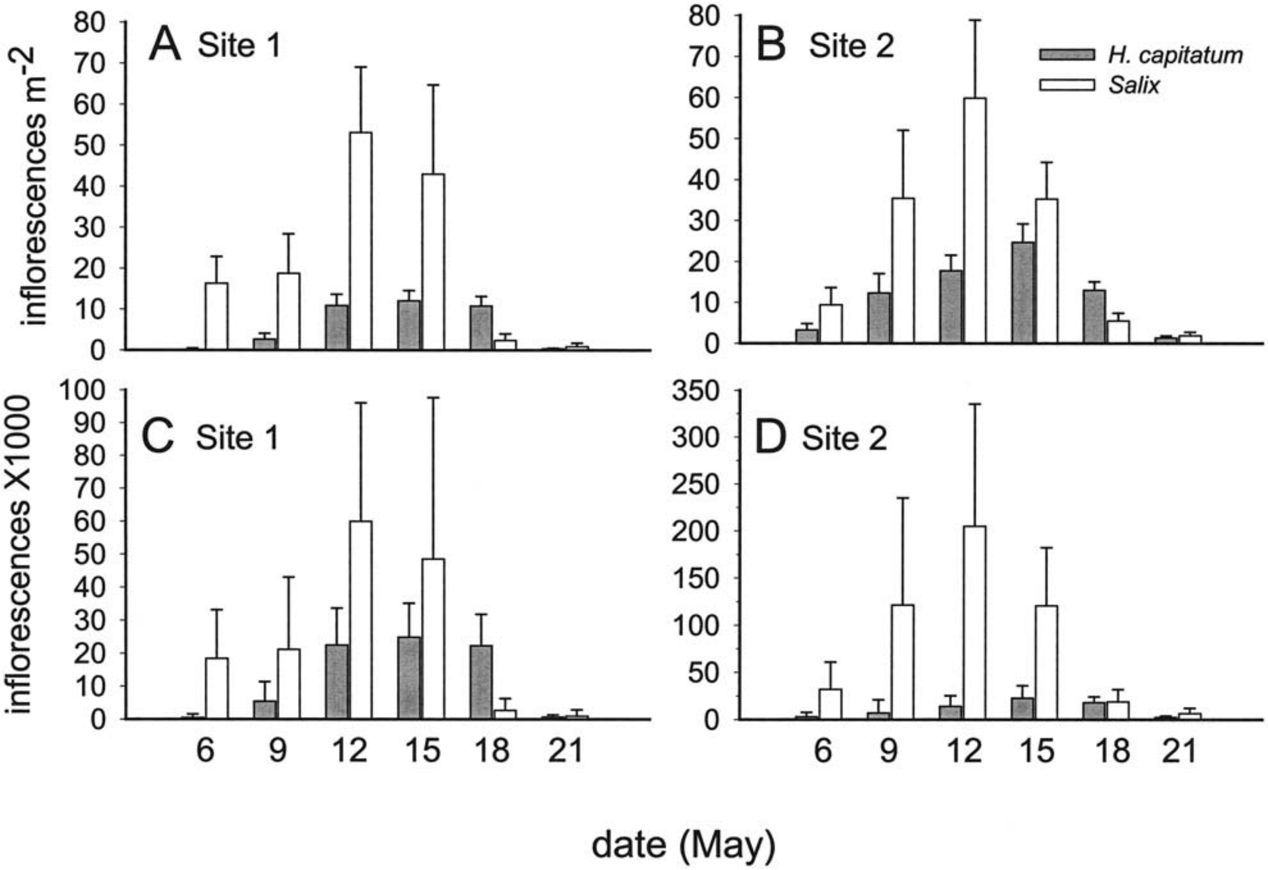

Figure 2
Resource phenology at Site 1 and Site 2. (A and B) The number of inflorescences (mean ± SE) per squared meter within patches of *Salix* and *Hydrophyllum capitatum* across sampling dates; $n = 20$ for each species and date. (C and D) Total inflorescences (±SE) per site calculated as [(mean inflor/m^2) × total area].

analysis for each date showed significant distance effects for May 15 and May 18 ($F_{2,214} = 14.23$, $p < .001$; $F_{2,214} = 3.32$, $p = .04$, respectively). Pollen collection by F1 bees was indistinguishable from S1, perhaps because the unequal distance to additional patches of *Salix* and *H. capitatum* to the west of the study site made *Salix* foraging more profitable than *H. capitatum* for F1 and F2 bees (Figure 1).

At Site 2, distance had no overall effect on *Salix* collection (Table 1), although during the first part of the season, bees at S2 clearly collected more *Salix* pollen than did bees at either H2 or F2 (Figure 4A). Distance affected *H. capitatum* collection weakly. Bees nesting at H2 collected significantly more *H. capitatum* pollen than did bees at S2 (Figure 4B $t = 4.27$, df = 3.89, $p_{\text{adj}} = .04$).

Resource density

The effect of resource densities on pollen collection depended on the pollen species and varied among sites. Contrary to our predictions, use of a pollen species sometimes responded negatively to its density.

Neither *Salix* nor *Hydrophyllum* density significantly affected bee's collection of *Salix* pollen, at either site (Table 1). Bees nesting at S1 and F1 locations tended to collect more *Salix* pollen during the middle of the season when it was most abundant (Figure 3A,D), whereas bees at H1 collected an invariant proportion of *Salix* pollen throughout the season. At Site 2, *Salix* use was completely independent of the density of either resource species (Figure 4A,D). S2 bees collected predominantly *Salix* pollen throughout the season, responding little to changing resource density. Bees nesting at H2 and F2 collected more *Salix* pollen during the second half of the season, despite its declining density (Figure 4D). Earlier, they foraged at *C. douglasii* and *H. capitatum* and switched to *Salix* pollen between May 9 and May 12, perhaps with decline of *C. douglasii* availability.

In contrast to *Salix* collection, collection of *H. capitatum* responded positively to its density at both sites (Table 1); however, the effect was weak and the pattern of use differed substantially between the sites. At Site 1, bees virtually ignored it early, to a degree favoring *C. douglasii* instead (Figure 3B,C). They then switched to *H. capitatum* midseason. The common movement by all bees to increase use of *H. capitatum* during the second half of the season was associated with precipitous declines in *Salix* and *C. douglasii* density compared with *H. capitatum* density (Figure 3D). The comparatively strong *Salix* decline also resulted in the significant interaction between *Salix* and *H. capitatum* densities (Table 1). Thus, *H. capitatum* likely did not achieve high enough resource profitability until later in the season, when the rate of provisioning by bees also dropped dramatically, from 342 cells per day by 152 females on May 15 to 98 cells by 119 females by May 21. At Site 2, *H. capitatum* use by bees at all nest locations tracked changes its density, but the effect was weak (Figure 4B and Table 1).

Provisioning rate

The rate of provisioning changed closely with inflorescence density. At both sites, females completed more brood cells per

Table 1

Results from generalized linear models testing the proportion of each pollen species collected by bees nesting at each location

		Site 1				Site 2			
		Salix		*H. capitatum*		*Salix*		*H. capitatum*	
Source	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Nest location (distance)	2	10.55	.05	0.55	.62	3.21	.20	6.21	.07
Salix density	1	0.95	.39	109.90	.01	1.19	.35	0.02	.88
H. capitatum density	1	3.76	.41	52.83	.01	1.45	.31	5.58	.06
Salix density × location	2	0.80	.53	0.69	.57	0.63	.60	0.88	.49
H. capitatum density × location	2	0.44	.68	1.05	.45	0.99	.48	0.43	.68
Salix × *H. capitatum*	1	0.86	.41	70.40	.01	3.61	.15	6.61	.04
Salix × *H. capitatum* × location	2	0.31	.75	0.09	.91	1.35	.40	2.59	.21

sampling period (3 days) as inflorescence density increased (Site 1: $b = 0.022$, $r^2 = 0.126$, $p < .001$; S2: $b = 0.030$, $r^2 = 0.101$, $p < .001$; H2: $b = 0.014$, $p < .001$; F2: $b = 0.008$, $p = .043$). Viewed over the foraging season (Figure 5), females increased provisioning rates during the middle of the season when resource densities were highest (Figure 2). At Site 1, there were no significant differences in the effect of inflorescence density on provisioning among nest locations; however, at Site 2, the effect depended on nest location (Figures 5 and 2; density × location effect; $p < .001$).

Pollen mixing

Distance to flower patches, and flower density had little effect on the overall incidence of pollen mixing. The majority of bees at all locations collected mixtures of pollen. Of the provisions at Site 1, 214 of 233 contained pollen mixtures, as did 202 of 250 at Site 2.

Contrary to our prediction, bees nesting within resource patches did not consistently construct fewer mixed provisions than those nesting in the field location (Figure 6). The tendency of bees to mix pollens differed between sites ($\chi^2 = 10.53$, df = 1, $p < .002$). At Site 1, bees at H1 made more mixed provisions than did bees at F1 and S1, although only the difference with F1 was significant (Figure 6). There was no trend in the number of mixed provisions made during the season. At Site 2, bees at H2 constructed significantly more mixed-pollen provisions than did bees at S2. Bees nesting at F2 did not construct significantly different numbers of mixed provisions than bees at H2 (Figure 6). In contrast to at Site 1, the number of pure provisions per sample date also increased during the season at all three locations. Twenty of the 48 provisions containing pollen of a single species were constructed on the last sample date. Most pure provisions (46 of 48) contained *Salix* pollen, even those from H2 (eight of 10).

Based on replicate samples from different points within provisions on three different dates at Site 2, bees commonly mixed pollen species within individual foraging trips. Only 27 of 98 provisions sampled contained replicates with pollen of a single species (Table 2). All of these provisions contained either *Salix* or *C. douglasii* pollen.

DISCUSSION

Effects of distance

We found only slight support for an effect of distance to resource on foraging behavior. When resources were naturally segregated into distant monospecific patches, female *O. lignaria* generally collected more of the near species compared with bees nesting far from that same species. Thus, it is likely that travel costs play a role in rendering distant patches less profitable to foragers. These results agree with previous studies of the effect of distance to resource patches on

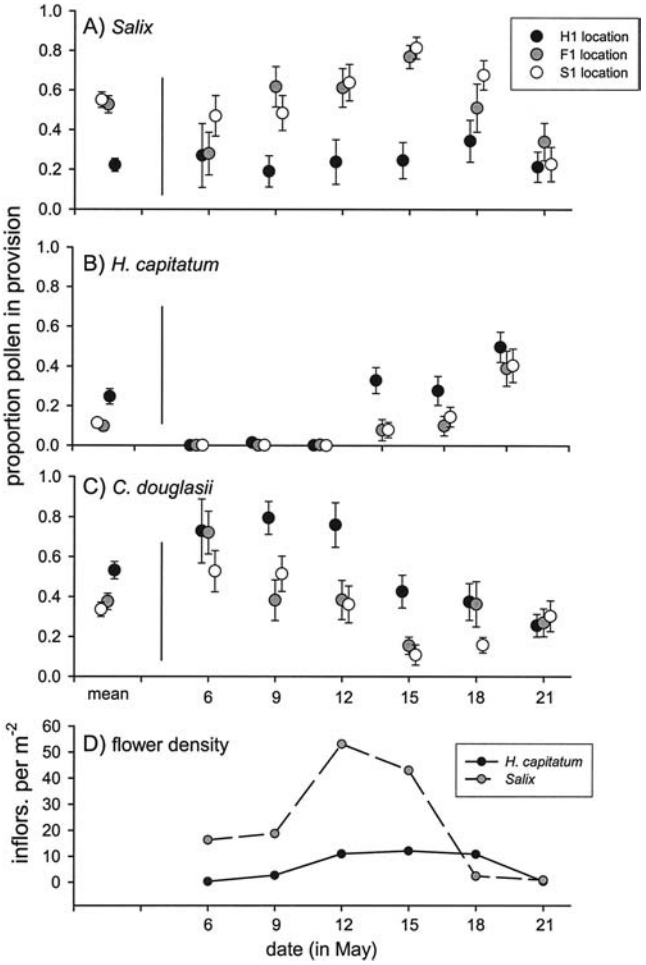

Figure 3
Site 1 pollen use and resource density during the flight season of *Osmia lignaria*. Proportions of three pollen species (mean ± SE) collected at S1, F1, and H1 nest locations on different sampling dates. In each panel the first point shows the mean ± SE for the entire season; n = 10–15 nests per date: *Salix* pollen (A), *Hydrophyllum capitatum* pollen (B), and *Crataegus douglasii* pollen (C). (D) Mean densities of *Salix* and *H. capitatum* inflorescences.

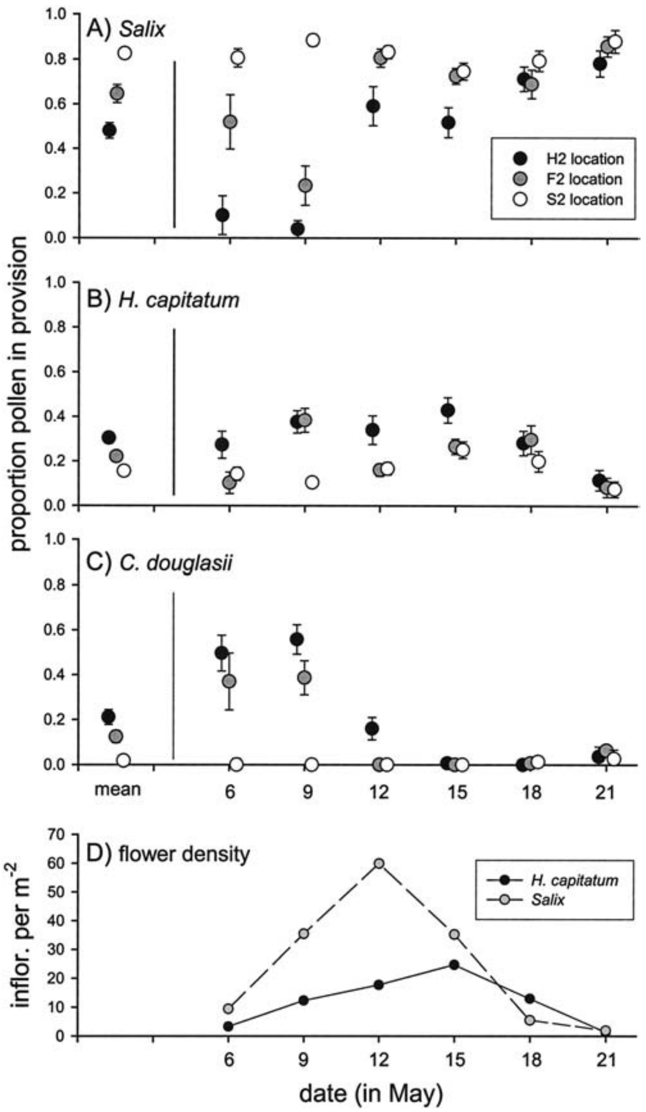

Figure 4

Site 2 pollen use and resource density during the flight season of *Osmia lignaria.* Mean ± SE proportions of three pollen species collected at S2, F2, and H2 nest locations on different sampling dates. In each panel the first point shows the mean ± SE for the entire season; n = 10–15 nests per date: *Salix* pollen (A), *Hydrophyllum capitatum* pollen (B), and *Crataegus douglasii* pollen (C). (D) Average densities of *Salix* and *H. capitatum* inflorescences.

foraging by birds and mammals (Brown and Morgan, 1995; Naef-Daenzer, 2000).

Resource availability

Although provisioning rate responded predictably to resource density, density did not affect the species of pollen used in any consistent way (Figures 3 and 4 and Table 2). Foraging theory predicts that resource use of a particular species is affected by the density or abundance of more profitable alternatives. Although the relation between use and density need not be linear, a positive relationship is expected (Stephens and Krebs, 1986). In our system, even predictions of the direction of response were not consistently met.

There are at least three explanations for the poor correspondence between pollen collection and availability. First, foragers might have been initially insensitive to developing changes in resource density, and might have delayed forsaking relatively unproductive patches for more rewarding ones until differences were more marked (Heinrich, 1976; Thomson, 1988, 1996; Thomson et al., 1982). Such delays have been attributed to the influence of long-term memory of resource location and quality (Thomson, 1996). To test for such a delay, we reexamined pollen use by using flower densities measured on the previous sampling date (i.e., with a lag of 3 days). The analysis did not consistently provide a better fit than did unlagged data; foraging by *O. lignaria* females may be more species or location persistent than we suspect, or it may be relatively insensitive to all but large resource changes.

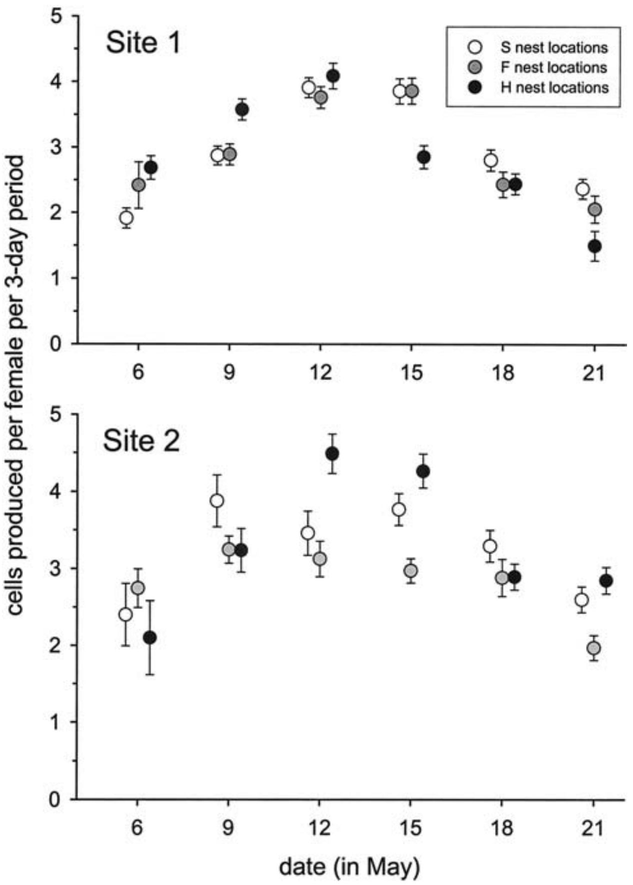

Figure 5

Rates of offspring provisioning (mean ± SE) throughout the season by *Osmia lignaria* females nesting at different locations at each study site. Sample sizes ranged from 12 to 92 nests per sampling date and location.

Second, our estimates of inflorescence density and abundance may not reflect the true availability of pollen to foraging bees. Data suggest that resources were superabundant only in mid-season (Figures 2 and 5), when they were associated with high provisioning rates; incorporating alternative species should have been unprofitable especially for that brief peak resource period, and we expected the incidence of mixed provisions to be lowest then, at least for S bees at both sites. However, peak provisioning rates were not associated with consistently low levels of mixing (Figure 5): 100% of sampled provisions collected by S1 bees on May 12 and more than 60% of provisions sampled on May 15 were mixed. Virtually all sampled provisions for H1 and H2 bees for these two site dates were also mixed. Average use of 10–30%

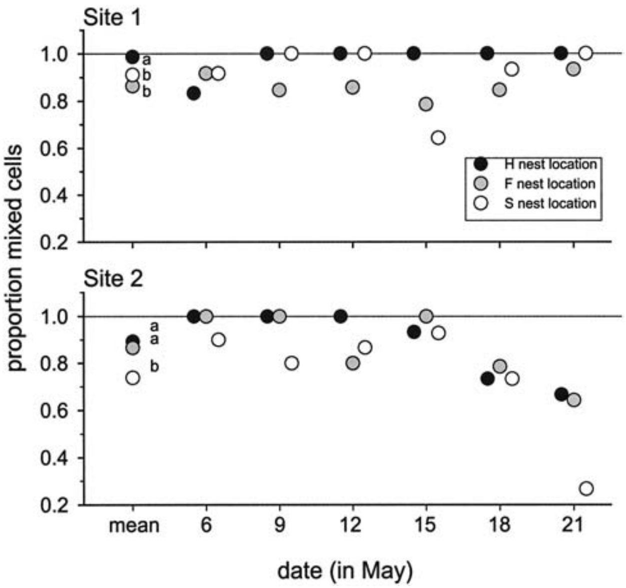

Figure 6
Proportion of cells containing mixtures of two or more pollen species constructed by females nesting at each location on different sampling dates at each site. The first set of points report mean values for each location. Different letters beside each point indicate significant differences $p < 0.05$ using paired comparisons and Dunn-Sidák methods for multiple tests. Number of nests sampled per location: n = 10–15 for May 6, n = 15 for all other dates.

H. capitatum pollen at all nest locations also suggests that some factor unrelated to economically efficient pollen collection is promoting mixing.

Finally, there can be little question that extensive collection of *C. douglasii* pollen contributed to the poor correspondence between *Salix* and *H. capitatum* density and pollen collection on some dates. *C douglasii* bloomed at least a few days earlier than did *Salix* and *H. capitatum* and peaked while their numbers were low. At Site 1, *C. douglasii* pollen remained a substantial component of provisions at all times, at all nest locations (Figure 3). At Site 2, its influence was diminished by mid-season (Figure 4). Nevertheless, bees at all locations collected mixtures of *H. capitatum* and *Salix* early, as they did throughout the rest of the season.

Pollen mixing

Although resources proximity and density affected bee foraging behavior in some instances, they offer limited insight into the overall pattern of use. The most striking pattern remains the consistent pollen mixing, which itself might have tempered distance and density effects. Female *O. lignaria* collected mixtures of pollen from flower species growing in distantly separated patches, usually within single foraging trips. Such inveterate mixing behavior, with its attendant increase in between-patch travel costs begs explanation. Why would females have traveled an extra 7.3–16.0 km, requiring up to 43 min per provision (based on flight speed of similar-sized *Apis mellifera*; Williams, 1999) to collect pollen from both species on each foraging trip?

Table 2

Number of provisions with at least one subsample containing pollen of only one species (pure) versus all replicates of mixed pollen

Nest locations	≥1 pure subsample	0 pure subsample
H2	5 (1)	27
F2	10 (6)	20
S2	12 (12)	24
Totals	27 (19)	71

Pure replicates include either *Salix* or *Crataegus douglasii* pollen. Numbers in parentheses are for samples containing pure *Salix* pollen.

One explanation is that each pollen species is nutritionally deficient alone (Bernays et al., 1994; DeMott, 1998). However, controlled feeding experiments have shown that *O. lignaria* larvae grow and survive equally well on diets of pure *Salix* pollen, pure *H. capitatum* pollen, or mixtures of the two (Williams, 1999). Thus, females do not appear to mix for reasons of pollen nutrition.

Bees might also include a less profitable pollen species in the diet as supply of the preferred species becomes depleted during the day. Although we did not assess pollen depletion directly, within-day shifts from one resource to others would be manifested as shifts within single provisions from one species to the other or to a mixture of pollens. Replicate samples from individual provisions indicated that bees switched from collecting pure loads of *Salix* to mixed loads in only nine of 90 provisions. Shifts from *H. capitatum* to mixtures never occurred. Most provisions (72.4%) were mixed throughout, indicating that bees mix within single foraging trips throughout the day. Depletion may have contributed to pollen mixing, but by itself it is an inadequate explanation.

A third explanation is that the need to collect both pollen and nectar concurrently favors visiting both *Salix* and *H. capitatum* on most foraging trips. This behavior is favored when two circumstances hold: (1) the profitability of pollen

Table 3

Pollen and nectar availability and handling times for single inflorescences of *Salix* and *Hydrophyllum capitatum*

	Salix		*H. capitatum*	
Parameter	Pollen	Nectar	Pollen	Nectar
Resource level	1,056,000 ± 390,100	0.30 ± 0.17 µl	983,000 ± 144,000	4.77 ± 1.78 µl
No. of open flowers	16.6 ± 6.4		8.83 ± 3.23	
Handling time, s	5.52 ± 1.57	15.58 ± 1.57	12.00 ± 0.89	31.88 ± 3.10

Values for pollen, nectar, and numbers of flowers are mean ± SD. Pollen is reported as number of grains. Visit durations are mean ± SE. *Sali*: pollen, n = 11 bees; nectar, n = 10 bees; *H. capitatum*: pollen, n = 13; bees, nectar, n = 17 bees, with two to four replicates per bee. Handling time includes interflower flight within the inflorescences. Females nearly always collected pollen and nectar during "nectar" visits to *H. capitatum*.

and nectar collection on the two species is reversed; and (2) efficient collection of one resource from a flower does not preclude efficient collection of the other. For example, some pollen harvesting from the good-nectar poor-pollen species is more efficient than collecting nectar only from one species and pollen only from the other. *Osmia lignaria* foraging at *Salix* and *H. capitatum* fits this description. Pollen rewards were nearly equivalent for the two species, but *H. capitatum* inflorescences contained over 10 times more nectar than *Salix* (Table 3). Bees visited *Salix* inflorescences twice as fast as *H. capitatum*, suggesting that *Salix* may be a more profitable pollen source and *H. capitatum* a more profitable nectar source. Additionally, bees actively collected pollen from *H. capitatum*, primarily while collecting nectar (Williams NM, unpublished data). The position of the bee during nectar foraging at *H. capitatum* placed the anthers in contact with pollen collecting hairs, so that pollen harvest did not require added time or repositioning the body. We suggest that the reversed profitability between the two essential nutrients creates a trade-off, such that bees constructed provisions fastest by dividing time between the two plant species despite the additional flight distance required. A foraging model that incorporates data on the inflorescence densities of each plant species and distances between patches predicts collection of pure *Salix* pollen when only the pollen resource is considered, but mixing of *Salix* and *H. capitatum* when the nectar resource is also included (Williams NM, unpublished). If nectar requirements indeed influence pollen foraging decisions, they add an unanticipated level of complexity to our understanding of pollen use by solitary bees.

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