PLANT ANIMAL INTERACTIONS

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Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae)

Abstract If trade-offs between flexibility to use a range of host species and efficiency on a limited set underlie the evolution of diet breadth, one resulting prediction is that specialists ought to be more restricted than generalists in their ability to use novel resource species. I used foraging tests and feeding trials to compare the ability of a generalist and a specialist solitary mason bee species to collect and develop on two pollen species that are not normally used in natural populations (novel pollens). *Osmia lignaria* (Hymenoptera: Megachilidae) is a generalist pollen feeder; *O. californica,* is more specialized. Adults of the specialist were more limited in use of novel hosts, but only in some contexts. Both bee species refused to collect one novel pollen. The specialist accepted a second novel pollen only when it was presented along with its normal pollen, whereas the generalist collected novel pollen whether presented alone or with normal pollen. Surprisingly, larvae of the specialist were more flexible than were generalists. The specialist grew well on mixtures of normal and novel pollen species, in some cases better than on its normal host alone. Larvae of the generalist grew more poorly on all diets containing novel pollens than on their normal host. Data on these two species of bees suggest that specialization by itself need not reduce flexibility on novel hosts. The findings also provide information about mechanisms of specialization in bees. Similar to some folivores, specific cues of the pollen host and the bee's interpretation of these contribute, along with foraging economics, to pollen choice by adults. The ability of the larvae to cope with specific components of one pollen species need not interfere with its ability to use others.

Introduction

Herbivorous insects are confronted with an array of alternative plants within the environment, some that are normally used as food hosts and others that are rarely if ever used in natural populations. The ability of adults and larvae to use these other "novel" hosts can influence population dynamics, allowing females to produce offspring when normal hosts are rare or absent (Thorp 1969; Cruden 1972; Parker and Tepedino 1982; Singer 1983; Thomas et al. 1987), and may allow the herbivore to expand its geographic range beyond that of the primary host (e.g., Cruden 1972; Estes and Thorp 1975; Thompson 1993). If variation in the ability to use novel hosts has a genetic component, it defines the potential for evolutionary changes in diet range through host shifts or expansion of the current host set (Thompson 1988; Via 1990).

Much of the research on the use of novel host plants has centered on diet specialization and the purported trade-off between efficient use of a limited number of hosts and reduced ability of adults and/or larvae to use alternatives. Investigations of adults and larvae generally have considered whether specialist species are more efficient on their preferred host plant than are related generalists (e.g., Strickler 1979; Futuyma and Wasserman 1981; Moran 1986). Less attention has been paid to the complementary prediction that specialists should be less flexible than generalists in their ability to use novel hosts. In the adult, selection for efficient recognition may enhance sensitivity to a limited number of cues used to distinguish preferred hosts (reviewed in Bernays 2001), but at the same time limit recognition of alternatives. Behavioral or morphological adaptations that facilitate efficient harvest of resources from preferred species (Strickler 1979; Thorp 1979) may further limit the ability of specialists to use novel hosts. There is increasing

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evidence for more efficient recognition by specialist adults (Bernays 2001), but it is uncertain if this reduces their ability to use alternative hosts. In the larvae, adaptation by specialists to efficiently use particular nutrients or cope with toxins might also limit alternative host use (e.g., Roininen and Tahvanainen 1989). Evidence for such trade-offs in performance of larvae on normal versus novel hosts is at best equivocal (reviewed in Jaenike 1990; Fry 1996; Thompson 1996). The uncertainty surrounding performance of generalists and specialists on novel resources, may be solved with further investigation. At the same time, additional insight into the use of novel hosts might be gained by examining a different type of herbivore.

Solitary bees as herbivores

Although they are rarely thought of as herbivores, bees rely entirely on plants for their food. Pollen collection by adult solitary bees and subsequent feeding by larvae parallel oviposition and feeding in numerous other insect herbivores in which females make food choices but larvae consume the food (e.g., Singer et al. 1988; Via 1990; Thompson and Pellmyr 1991; Fox et al. 1997). As is true for diet specialization among other herbivorous insects, pollen specialization in bees spans a continuum. At one end are generalists that use pollen from a number of plant species across multiple families, at the other are specialists whose populations restrict pollen collection to several plant species within one or a few related genera, even when other sources are available (Linsley 1958). Despite an extensive literature on novel host use and specialization in folivores, little is known about the role of adult or larval traits for determining novel pollen use by bees (Levin and Haydak 1957; Cruden 1972), or how use of novel pollen species might vary with the degree of dietary specialization.

The mutualistic quality of bee-plant interactions suggests that pollen use by bees might be subject to different selection pressures than host use by herbivores; however, antagonistic aspects that limit host use in other herbivore-plant interactions also operate in bee-plant systems (Kearns et al. 1998). Bees vary in quality as pollinators and can actually steal resources and reproductive potential from plants (Thomson and Thomson 1992; Irwin et al. 2001; Williams and Thomson, unpublished data). Pollen, like other plant tissue, varies tremendously in nutrients (Stanley and Linskens 1974; Roulston et al. 2000) and in some cases contains secondary compounds that may limit use by certain bee species (Detzel and Wink 1993).

Unlike most folivores, adult female bees collect the resources for their offspring during foraging trips to many individual plants. Resource collection magnifies the importance of foraging efficiency for determining host use, and also enables females to provision single offspring on mixtures of pollen species (Cripps and Rust 1989; Bullock et al. 1991; Williams and Tepedino 2003). In this sense bees are grazers (see Thompson 1994). From the larval perspective, mixing implies that except where normal hosts are absent, larvae will likely encounter novel species of pollen piecemeal along with normal pollen species rather than as pure diets. Piecemeal encounter with novel pollens may have profound implications for novel pollen use and the evolutionary lability of diet range. Normal pollen in the provision might mitigate negative effects of novel pollen, such as toxicity or lack of required nutrients. As a result, larval performance is less likely to limit novel host use in solitary bees than in herbivores that cannot mix, and selection against use of novel pollen should be weak. Selection also might favor incorporation of a novel pollen species when it is mixed with normal species even though the novel pollen is unpalatable as a pure diet.

I investigated the use of one normal and two novel pollen species by two closely related species of solitary bees that differ in pollen specialization. *Osmia lignaria* is considered a pollen generalist, collecting pollen from a wide range of flower species across several families (Rust 1974). *Osmia californica* is more specialized, restricting pollen collection to a few species of Asteraceae within the tribe Heliantheae (Cripps and Rust 1989). I used surveys of pollen use by natural populations, adult behavioral assays and larval feeding experiments to test the hypothesis that use of novel pollens is more restricted in specialists than in generalists. I also explore the role of adult and larval traits in determining novel-pollen use and consider whether patterns for bees are similar to those found in other herbivorous insect groups.

Materials and methods

Bee species

Osmia lignaria and *O. californica* are sympatric and have overlapping flight seasons throughout much of their ranges, the former preceding the latter by 3–4 weeks. *Osmia lignaria* commonly collects pollen from *Salix* spp. (Salicaceae), *Hydrophyllum capitatum* and *Phacelia* spp. (Hydrophyllaceae), and spring-flowering Rosaceae (Rust 1974; Cripps and Rust 1989). *Osmia californica* in northern Utah collects pollen almost entirely from three Heliantheae species *Balsamorhiza macrophylla*, *Wyethia amplexicaulis* and *Helianthella uniflora*, sometimes turning to *Cirsium* species later in its flight season. At my study locations, the three Heliantheae species occur in mixed patches and individual females collect pollen from all three within single foraging bouts. For experiments, I used mixtures of the three and refer to them as a group, Heliantheae, throughout the paper. Bees used in the experiments were collected in "trapnests" (Krombein 1967) from populations in the Cache Valley, Cache Co., Utah, USA. Experiments were conducted at the USDA Bee Biology and Systematics Laboratory, Logan, Utah.

Both species nest in tunnels within wood and will readily accept as nest sites "artificial" holes that have been drilled into blocks of wood. Nests are constructed as a linear series of brood cells each of which contains a single egg along with a provision of pollen and nectar. By lining holes with paper drinking-straws, the entire nest could be temporarily removed without interrupting nesting females. This procedure allowed me to record nesting progress on the outside of the straw. I could also sample pollen from individual brood cells and manipulate individual eggs and larvae by carefully slicing open the sides of the nest.

Pollen use in natural populations

I sampled pollen from nests of *O. lignaria* at two locations in 1995 and from *O. californica* at two locations in 1995 and two in 1997. All sites were located in the Cache Valley at approximately 1,550 m elevation. For each population, I sampled pollen from three provisions per nest, from a random sample of nests completed on different dates. Within nests, random samples were stratified across regions of the nest (front, mid, rear) to encompass pollen collected throughout the construction of the entire nest. Samples were collected as fresh pollen or remnants from fecal pellets. Fresh pollen was mounted directly in glycerin gelatin stained with basic fuchsin (Beattie 1971). Fecal-pellet samples were acetolyzed (Erdtman 1969) before mounting. I scored the number of grains of each pollen species in a sample of 200 from each provision using a compound microscope and a reference collection made at the time of the study. Counts from the three provisions were pooled to calculate the proportion of each pollen species collected per nest.

Tests of novel pollen collection

For each bee species I measured variation in the collection of two novel pollen species using combinations of choice and no-choice tests. Because there is no overlap in the pollens collected by natural populations of the two bee species, I used a reciprocal design in which the normal pollen-host of one bee served as one of the novel pollens for the other. *Phacelia tanacetifolia* was the normal pollen for *O. lignaria* and the novel pollen for *O. californica*; Heliantheae was the normal pollen for *O. californica* and novel for *O. lignaria*. *Brassica oleracea* served as the other novel pollen for both bee species. Although it does not grow naturally in Utah, *Phacelia tanacetifolia* is native to California and *O. lignaria* females readily accept it where the bee and plant co-occur.

Each experiment presented host plants to each female in a three-phase design: Choice (normal with novel), No Choice (novel only), and Choice (the normal and same novel again). The second choice phase was included to control for potential differences in bees' response due to aging or experience. Each phase lasted 4 days. I reintroduced the novel host (Choice phase 2) during the middle of the day, so that bees' behavior during the reintroduction could be observed.

I used potted *P. tanacetifolia*, *Brassica oleracea* and *Helianthus annuus* var. Perdovik plants. *Helianthus annuus* (tribe Heliantheae) was supplemented with freshly cut *Balsamorhiza macrophylla* and *Helianthella uniflora*. These wild Heliantheae were cut late every afternoon and placed into the cages at sundown in preparation for the following day's experiment. Cut flowers contained natural volumes of nectar (*B. macrophylla* 0.189±0.155 µl per floret, *H. uniflora* 0.110±0.081 µl per floret, ~ 8–20 open florets per head) and presented fresh pollen the day after cutting. I attempted to equalize the amount of each flower species available and provide enough bloom so that foraging was not unnaturally resource limited. Both pollen and nectar remained in flowers at the end of the day, and provisioning rates were consistent with natural conditions (Williams and Tepedino 2002, unpublished data). Nevertheless, during Choice treatments resources of any single species would likely have become depleted to a point where incorporating the alternative would have been the most profitable foraging strategy. During No Choice phases the number of flowers of the novel resource was increased to compensate for the removal of the normal host species.

During the experiments, females foraged in large flight cages (6.1×6.1×1.7 m or 7.6×7.6×3 m). Females were released into the first Choice phase as they emerged from their cocoons and so were naïve to any floral resources. Males had been released the previous afternoon and were removed once mating had occurred and females had begun nesting. On each of the 4 days per phase, I monitored foraging and nesting activity for 1 h in the morning and 1 h in the afternoon (8 h per phase). At the end of each day, I recorded the number of brood cells completed by each female (Williams and Tepedino 2002). At the end of the experiment, I carefully opened the nest cells and sampled pollen from the front and rear of each provision completed during the Choice phases. Pollen was prepared and scored as in natural nest surveys. Measurement of use was based on the pooled sample from each provision.

I compared the cell provisioning among Choice and No Choice phases using repeated measures ANOVA. I tested the difference in the proportion of each pollen species used between the two Choice phases using Friedman's method for randomized blocks (Sokal and Rohlf 1995) to account for repeated measure of individual bees between phases.

Larval performance on normal and novel pollen diets

To measure the performance of larvae on novel species of pollen, I transferred eggs from completed nests to diets that contained mixtures of normal and novel pollen and then reared larvae until emergence. Five mixtures, determined by weight, were used for each novel pollen: 100% normal, 80%:20% normal to novel, 50%:50% normal to novel, 20%:80% normal to novel, and 100% novel.

All diets contained bee-collected pollen and 1:1 glucose – fructose solutions (50% total sugar by mass) and were prepared to achieve a consistency comparable to that of natural provisions (45% nectar, 55% pollen by fresh mass; Williams, unpublished data). I gathered fresh Heliantheae and *P. tanacetifolia* pollens from *Osmia* nests as needed, and used *B. oleracea* from honey bee corbicular pellets stored frozen until mixing. All source pollens were sampled microscopically to insure that they contained only the desired species before I mixed experimental pollen diets. Once mixed, diets were stored at 4°C and used within 3 days. *Osmia lignaria* were provided 0.25 ml of provision and *O. californica* 0.35 ml. Provision volumes were determined from samples of wild-collected provisions of each bee species.

I collected eggs from nests constructed by females at the same sites where pollen use was monitored. All nest holes were lined with a paper straw so that I could extract completed nests without damaging the contents. Nests, within straws, were opened in the laboratory under semi-sterile conditions. I transferred the egg from each cell to a standard volume of handmade provision contained in a 0.5 ml plastic cup. Once transferred, the eggs and provisions were placed into petri dishes and incubated at constant temperature through pupation (25°C for *O. lignaria* and 28°C for *O. californica*; *O. californica* flies later in the spring and so encounters higher average temperatures during development). Once they have provisioned the brood cell, female *Osmia* do not interact with the egg or developing larvae so that lab rearing did not differ substantially from the developmental conditions in natural populations. In mid October cocoons were moved to a 4°C incubator for the "winter". *Osmia lignaria* were warmed the following May and *O. californica* the following June. All cocoons were first warmed to 10°C for 7 days, then maintained at 25°C:20°C day: night until emergence.

I scored three indices of performance: mass of the 5th instar larvae during cocoon spinning (larval mass), number of days from egg to cocoon spinning (development time) and survival from egg to emergence (survival). As larvae begin to spin the cocoon, they eject remaining feces, so at this time mass is least biased by pollen and nectar remaining within the gut, but larvae can still be weighed without affecting subsequent cocoon spinning. Larval mass, which correlates strongly with adult size, is likely to be a particularly good measure of fitness. The size of adult females positively affects fecundity, offspring size and offspring survival (Tepedino and Torchio 1982; Sugiura and Maeta 1989; Visscher and Danforth 1993; Kim 1997), and in males size can affect mating success (Torchio 1989; Alcock 1995).

To test the ability of larvae of each bee species to use novel pollens, I regressed larval mass and development time on the percent novel pollen in the diet. I used orthogonal contrasts between individual mixtures to examine non-linearities in the relationship. Mass and development time were log-transformed to normalize the data. In natural nests of *Osmia*, larval size negatively correlates with position in the nest (Rau 1937; Klostermeyer et al. 1973); larvae provisioned earlier are larger than those provisioned later. In part, this relationship arises because female offspring,

which are larger, tend to be positioned before males within nests. I randomized larvae from different positions within nests among the pollen mixtures to avoid nest position effects.

I measured survival of *O. lignaria* among mixtures using logistic regression with dummy variables for each level of mixture (Sokal and Rohlf 1995). I could not compare survivorship for *O. californica* because most larvae switched to a multi-year prepupa phenotype. In this phenotype pupation is delayed for 2–3 seasons (Torchio and Tepedino 1982), and so offspring could not be scored for emergence.

Results

Pollen use in natural populations

Pollen use in natural populations agreed with previous surveys for the two species (Cripps and Rust 1989). The generalist *O. lignaria* collected pollen from various plant families: Salicaceae (*Salix* spp.); Hydrophyllacae (*Hydrophyllum capitatum* and *Phacelia* spp.); and Rosaceae (*Purshia tridentata*; Table 1). Trace amounts of Heliantheae pollen were also present in 4 of 27 nests (<3% Heliantheae in one provision of each nest). This amount of pollen may have been a contaminant incidentally picked up by the female while foraging for nectar at this species (Rust 1974). The only Brassicaceae pollen present was *Isatis tinctoria*, which occurred in 5 of 27 nests at between 3% and 20%. Other studies have reported both Brassicaceae and *Taraxacum* sp. (Asteraceae) pollens in the nests of *O. lignaria* when these resources dominated the floral community (Torchio 1976, 1985).

Osmia californica collected predominantly Heliantheae (mixtures of *Balsamorhiza macrophylla*, *Wyethia amplexicaulis*, *Helianthella uniflora*) and Cirsi-
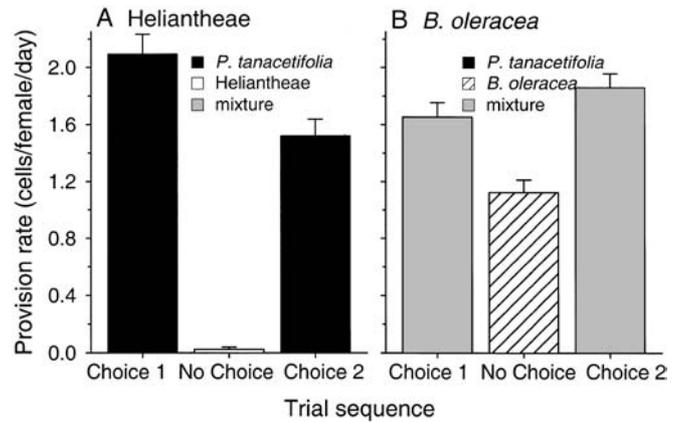

Fig. 1A, B Number of cells (mean±SEM) completed per female per day by *Osmia lignaria* during First-Choice, No-Choice and Second-Choice trials. Experiments with **A** Heliantheae (*n*=13) and **B** *Brassica oleracea* (*n*=14) as the novel pollen host. The shading of the *bars* indicates the type of pollen collected by bees during each experimental phase

um spp. (Table 2). Nests varied in the amount of novel pollen they contained. Much of the variation in pollen collection resulted from seasonal changes bloom, in particular the onset (site 1) or decline (site 2) of Heliantheae flowering at the site. At site 1, bees initially used *Taraxacum* sp. and *Tragopogon* sp. pollen, but shifted to almost pure Heliantheae collection. At site 2, *Cirsium* species bloomed slightly later than the Heliantheae; *Cirsium* sp. pollen was found only in nests completed late in *O. californica*'s flight season. One nest at site 2 contained 15.5% *Salix* and 24.7% Rosaceae pollen (Table 2). Other studies of *O. californica* in natural populations report only traces of non-Heliantheae pollen in all cells examined (Cripps and Rust 1989).

Adult collection of novel pollens

Both bee species rejected one species of novel pollen and accepted the other. The generalist, *O. lignaria,* rejected Heliantheae pollen during Choice and No-Choice phases of the experiment. Females actively provisioned offspring during Choice phases (Fig. 1a), but they used almost exclusively *P. tanacetifolia*, their normal host, to do so. Four of 13 *O. lignaria* nests contained a single cell with trace amounts of Heliantheae pollen (<3.5% in one
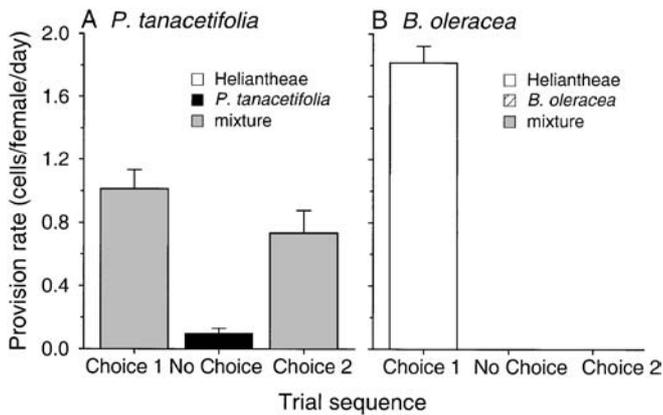
Table 1 Mean (SEM) percent of each pollen species collected by *Osmia lignaria* at two sites between 16 May and 20 June 1995

Pollen	Site 1 *n*=11		Site 2 *n*=16	
Salix sp.	73.9	(9.7)	68.2	(12.6)
Hydrophyllum capitatum	8.1	(4.3)	21.8	(7.9)
Phacelia sp.	7.7	(7.7)	0.5	(0.2)
Purshia tridentata	4.2	(1.5)	5.3	(3.3)
Prunus sp.	2.9	(1.5)	0.13	(0.1)
Fragaria sp.	0.0	(0.0)	0.2	(0.2)
Other Rosaceae	1.1	(1.1)	2.6	(1.6)
Isatis tinctoria	1.3	(0.9)	1.5	(1.5)
Heliantheae	0.1	(<0.1)	0.4	(0.2)
Unknown	1.2	(0.4)	0.0	(0.0)

Table 2 Mean (SEM) percent pollen collected by *O. californica* at two sites between 20 May and 30 June 1995 and 1997

Pollen	1995				1997			
	Site 1 *n*=6		Site 2 *n*=4		Site 1 *n*=44		Site 2 *n*=20	
Heliantheae	78.7	(17.5)	74.3	(21.2)	87.7	(4.6)	87.7	(5.7)
Cirsium sp.	18.9	(17.9)	21.6	(21.9)	0.0	(0.0)	10.9	(5.6)
Taraxacum/Trogopogon	2.3	(1.3)	0.8	(0.7)	12.3	(4.6)	0.2	(0.1)
Salix sp.	0.0	(0.0)	1.3	(1.5)[a]	0.0	(0.0)	0.0	(0.00)
Rosaceae	0.0	(0.0)	2.1	(2.4)[a]	0.0	(0.0)	0.1	(<0.1)
Isatis tinctoria	0.0	(0.0)			0.0	(0.0)	0.9	(0.3)

[a] Represented by a single nest

Fig. 2A, B Number of cells (mean±SEM) completed per female per day by *O. californica* during First-Choice, No-Choice and Second-Choice trials. Experiments with **A** *Phacelia tanacetifolia* (*n*=12) and **B** *B. oleracea* (*n*=10) as the novel pollen-host. The shading of the *bars* indicates the type of pollen collected by bees during each experimental phase
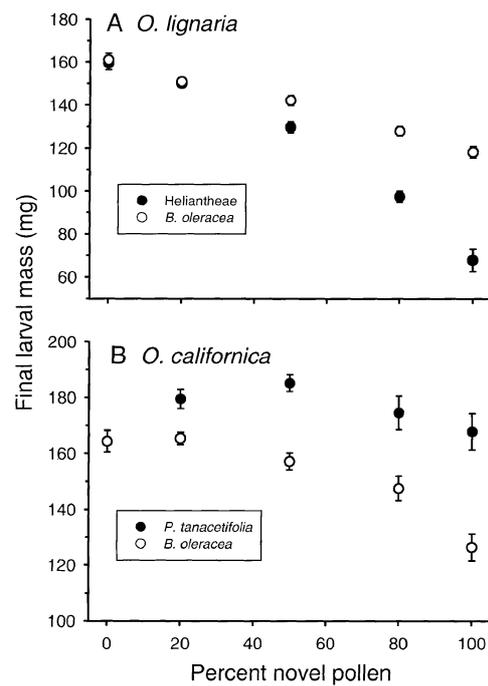

Fig. 3 A Final larval masses (mean±SEM) for *O. lignaria* grown on mixtures of *P. tanacetifolia* (normal) and one of two novel pollen types, Heliantheae or *B. oleracea*. *P. tanacetifolia*–Heliantheae mixtures 0% *n*=30; 20% *n*=36, 50% *n*=37; 100% *n*=14; *P. tanacetifolia*–*B. oleracea* 0% *n*=28, 20% *n*=36, 50% *n*=41, 80% *n*=31, 100% *n*=28. **B** Final larval masses (mean±SEM) for *O. californica* grown on mixtures of Heliantheae (normal) pollen and one of two novel pollen types, *P. tanacetifolia* or *B. oleracea*. Heliantheae–*P. tanacetifolia* mixtures 0% *n*=25; 20% *n*=27, 50% *n*=31, 80% *n*=34, 100% *n*=20; Heliantheae–*B. oleracea* 0% *n*=24; 20% *n*=32, 50% *n*=32, 80% *n*=34, 100% *n*=20

provision, 1% each of the other three) likely to have been acquired inadvertently while nectar collecting. I observed only one visit to Heliantheae during which the bee did not collect pollen. During the No-Choice phase, females ceased nesting (Fig. 1a). Two individuals that were left with partially completed provisions at the end of the first Choice phase abandoned their efforts. By the second day all bees had sealed their nest entrances. Bees collected nectar at Heliantheae during the No-Choice phase and in the process became partially covered with pollen. These bees would land on nearby foliage and fastidiously groom the pollen off before continuing to fly about the cage. Behavior changed dramatically following reintroduction of *P. tanacetifolia* flowers at the onset of the second Choice phase. Within 2 min, bees began to actively collect pollen and nectar from *P. tanacetifolia*. Even though plants were introduced in mid-day, seven bees completed cells on that day.

The specialist, *O. californica*, rejected the novel pollen, *B. oleracea* (Fig. 2b). For this experiment, only a single Choice phase was used due to accidental pesticide poisoning of the cages. During 6 h of observation over 3 days, I observed only a single visit to *B. oleracea* and only trace amounts of *Brassica* pollen (<1%) were detected in two provisions.

Each bee species accepted its other novel pollen, although the context of acceptance differed between the two. Both species accepted the novel pollen during the Choice phases (*O. lignaria* mean *B. oleracea* pollen ± SEM, Choice 1=16±4.2%, Choice 2=22±5.8%, *n*=14 bees; *O. californica* mean *P. tanacetifolia* pollen ± SEM, Choice 1=31.09±0.04%, Choice 2=17.27±3.83%, *n*=7). There was considerable variation among females in the amount of novel pollen collected, but use did not differ significantly between phases (*O. lignaria* $X^2_{[13]}$=1.14, *P*=0.29; *O. californica* $X^2_{[5]}$=1.67, *P*=0.10 Friedman randomized blocks). *Osmia lignaria* also col-

lected *B. oleracea* pollen and nested during the No-Choice phase (Fig. 1). The provisioning rate dropped from 1.65±0.10 cells per day during the first Choice phase to 0.43±0.14 cells during the first No-Choice day on *B. oleracea*, rebounding to 1.69±0.22 cells per day by the second day. The drop suggests that bees may have been using *B. oleracea* primarily for nectar during the Choice tests and learned to gather its pollen more efficiently. Unlike *O. lignaria*, *O. californica* ceased provisioning during the No-Choice phase (Fig. 2). The small amount of provisioning recorded during the No-Choice treatment was due to three females that infrequently collected pollen. They deposited only tiny amounts in their nests and did not initiate any new provisions

Larval performance on novel pollens

Offspring growth on novel pollen species differed substantially between the generalist and specialist and did not match predictions based on trade-offs. *Osmia lignaria* larvae fared worse on both novel pollens than on normal pollen. Larval mass decreased significantly and development time increased significantly with increasing

percentages of both Heliantheae and *B. oleracea* in the diet (Figs. 3a, 4a; Table 3). For both metrics the effect was stronger for Heliantheae than for *B. oleracea* pollen. Survivorship from hatching to emergence also decreased for larvae reared on novel pollens compared to on *P. tanacetifolia* (Fig. 5; $\beta=-0.3\%$, per percent increase in novel pollen, $P<0.01$). Survival rates did not differ between novel pollens.

In contrast to the generalist, larvae of the specialist, *O. californica*, actually grew better on some diets containing novel pollen than they did on normal pollen (Fig. 3b). Performance depended on the novel-pollen species (Table 4). Mass of larvae did not decrease with increasing amounts of *P. tanacetifolia* pollen [$F_{[1, 120]}=0.34$, $P=0.56$]. The effect was non-linear; larvae reared on mixtures containing 20% and 50% *P. tanacetifolia* actually grew larger than those fed pure Heliantheae pollen [$t_{[56]}=-2.28$, $P=0.024$; $t_{[54]}=-3.08$, $P=0.002$; orthogonal contrasts]. Larvae also developed equally quickly on diets containing up to 80% *P. tanacetifolia* pollen, so that the overall effect of increasing *P. tanacetifolia* pollen on development time was only weakly detrimental [$\beta=0.022$ days per percent increase of *P. tanacetifolia* pollen; $F_{[1, 119]}=28.99.23$, $P<0.01$; Fig. 4b]. *Brassica oleracea* was a poorer novel host than *P. tanacetifolia*. Larval mass decreased with increasing *B. oleracea* in the diet [$\beta=-3.7$ mg per percent *B. oleracea*; $F_{[1, 134]}=57.96$, $P<0.01$] and development time increased [$\beta=0.05$ days per percent *B. oleracea*, $F_{[1, 134]}=94.0$, $P<0.01$]. Again,
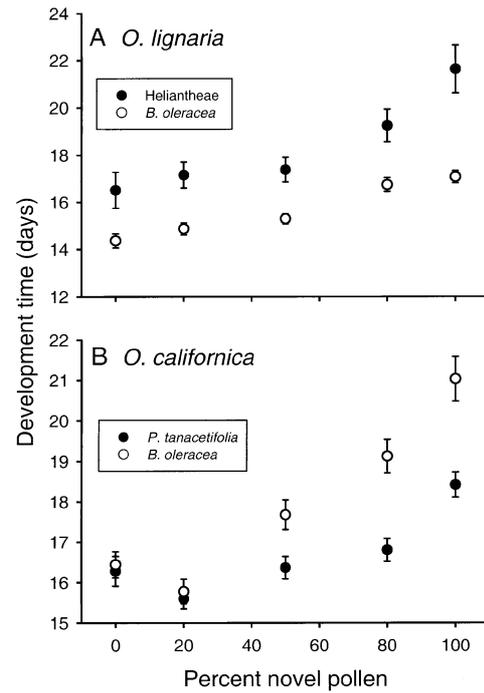

Fig. 4 A Development time (mean±SEM) from hatching to cocoon spinning for *O. lignaria* grown on mixtures of *P. tanacetifolia* (normal) and one of two novel pollen types, Heliantheae or *B. oleracea*. *P. tanacetifolia*–Heliantheae mixtures 0% *n*=30; 20% *n*=36, 50% *n*=32, 80% *n*=37, 100% *n*=14; *P. tanacetifolia*–*B. oleracea* 0% *n*=28, 20% *n*=36, 50% *n*=41, 80% *n*=31, 100% *n*=28. **B** Development time (mean±SEM) from hatching to cocoon spinning for *O. californica* grown on mixtures of Heliantheae (normal) pollen and one of two novel pollen types, *P. tanacetifolia* or *B. oleracea*. Heliantheae–*P. tanacetifolia* mixtures 0% *n*=25; 20% *n*=27, 50% *n*=31, 80% *n*=34, 100% *n*=20; Heliantheae–*B. oleracea* 0% *n*=24; 20% *n*=32, 50% *n*=32, 80% *n*=34, 100% *n*=20

there were non-linear effects. Larvae grew equally on mixtures up to 20% *B. oleracea* pollen (Figs. 3b, 4b).

For both bees, development was slower on all mixtures of novel pollen, but the delay (maximum ≅5 days) accounted for a small fraction of total development and was not of a magnitude that would likely affect bees' fitness. Both species reached a prepupal stage in 14–20 days and then remained in this stage until pupation occurred over two months later. As discussed above
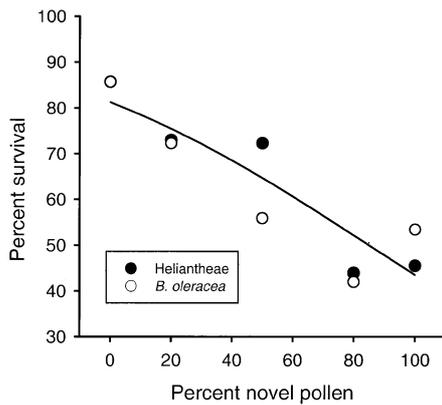
Table 3 Two-way analyses testing the effect of increasing percentage of Heliantheae or *Brassica oleracea* pollen in diet on larval mass and larval development time of *O. lignaria*

Source	df	SS	MS	F ratio	P
Larval mass					
Novel pollen species	1	0.089	0.089	6.73	0.01
Percent novel pollen	1	2.626	2.626	198.70	<0.01
Novel species × % novel	1	0.786	0.786	59.50	<0.01
Error	259	3.423	0.013		
Development time					
Novel pollen species	1	0.053	0.053	15.84	<0.01
Percent novel pollen	1	0.238	0.238	71.15	<0.01
Novel species × % novel	1	0.003	0.003	1.04	0.31
Error	256	0.572	0.003		

Table 4 Two-way analyses testing the effects of increasing percentages of *Phacelia tanacetifolia* or *B. oleracea* pollen on larval mass and development time of *O. californica*

Source	df	SS	MS	F ratio	P
Larval mass					
Novel pollen species	1	0.007	0.007	1.77	0.18
Percent novel pollen	1	0.119	0.119	32.81	<0.01
Novel species × % novel	1	0.085	0.085	22.01	<0.01
Error	253	0.978	0.004		
Development time					
Novel pollen species	1	1.40×10^{-4}	1.40×10^{-4}	2.07	0.79
Percent novel pollen	1	0.233	0.233	118.09	<0.01
Novel species × % novel	1	0.029	0.029	14.48	<0.01
Error	251	0.495	0.02		

Fig. 5 Survivorship from egg to emergence for *O. lignaria* reared on mixtures of *P. tanacetifolia* and either Heliantheae or *B. oleracea* pollen

(Materials and methods), mass is likely to be the better metric of fitness.

Discussion

Use of novel pollens by specialists and generalists

Results from *O. lignaria* and *O. californica* suggest that when adult and larval traits are considered together specialization need not reduce the ability of a bee species to use novel pollen species. Adults of the specialist *O. californica* were more limited in collection of novel pollen, but only in some contexts. Both species refused to collect one novel species of pollen. The generalist *O. lignaria* readily collected the other novel species in Choice and No-Choice trials. *Osmia californica* also collected one novel species, *P. tanacetifolia*, but only when its normal host, Heliantheae, was also present. More dramatic refusal to collect novel pollen has been demonstrated for the specialist bee *Hoplitis anthocopoides* (Strickler 1979). This species collected pollen significantly more efficiently from its preferred pollen-host (*Echium vulgare*) than did related generalists; however, it refused to collect pollen from alternative hosts. In my system, it was not possible to quantify increased efficiency by the specialist on the normal host because the generalist would not collect pollen from this species.

The results for larval performance were more striking than those for collection by adults. Larvae of the specialist actually grew better than did those of the generalist on the novel pollens. *Osmia californica* grew equally well on diets containing up to 50% *B. oleracea* pollen and grew at least as well on all mixtures containing *P. tanacetifolia* pollen as on pure Heliantheae, the normal pollen host. *Osmia lignaria* larvae were smaller when fed increasing amounts of either novel pollen. Thus, specialization per say does not necessarily lead to a trade-off in the ability of larvae to use novel pollen species.

If instead acceptable pollens are determined by presence or absence of specific nutrients or toxins (as has been shown for numerous herbivores) then the ability of bees to recognize or develop on novel species may depend on the similarity of relevant chemicals between normal and novel pollen. The reciprocal experimental design, in which the normal pollen of one bee species was used as the novel pollen for the other, was intended to equalize the novelty (i.e., degree of chemical and physical difference) of the novel pollens for the two bee species. However, the results of this study reinforce the idea that a chemical barrier need not operate equally in both directions. As has been pointed out for herbivores in general (Futuyma and Moreno 1988), adaptation to use one type of host need not limit performance on others.

Pollen nutrients and toxins

Some of the differences in performance between the specialist and generalist larvae on alternative pollens were likely due to differences in the nutritional quality of the pollen. Protein content, which is known to affect offspring size (Roulston, unpublished data), differed among pollens representative of those in my study (*Phacelia campanularia* 59%, *Brassica* spp. 31.9–33.6%, *Helianthus annuus* 30.6% (Roulston et al. 2000). Lower protein levels could contribute to the smaller size of *O. lignaria* fed diets containing *B. oleracea* and Heliantheae, but protein alone cannot explain the patterns. Protein levels in Heliantheae and *Brassica* species differed by only a few percent, but larvae were 74.1% smaller on average when reared on Heliantheae. Based on protein, *O. californica* also should have grown larger on diets that contained more *P. tanacetifolia* pollen and should have grown equally well on *B. oleracea* pollen. Instead, larvae grew larger only on intermediate mixtures of *P. tanacetifolia* pollen and smaller on *B. oleracea* pollen (Fig. 3b).

The patterns of larval growth on mixtures (Fig. 3) suggest a balance between nutrients and toxins in mixed diets analogous to the situation in some folivores (Pennings et al. 1993; Bernays et al. 1994; Bernays and Minkenberg 1997). *Phacelia tanacetifolia* and *B. oleracea* may have contained chemicals that inhibited growth of *O. californica*. Because *P. tanacetifolia* contained more protein, growth was highest at intermediate Heliantheae–*P. tanacetifolia* mixtures. Larvae fared worse on diets of increasing *Brassica oleracea* because it did not have a higher protein content than Heliantheae. Likewise, for *O. lignaria*, there was no toxin–nutrient balance; both novel species had lower protein than *P. tanacetifolia* and larvae grew worse as the proportion of novel pollen in the diet increased.

One potential "toxin" in the case of Heliantheae pollen might be the pollenkitt oil coating the grains, or some chemical within these oils. *Osmia californica*, which commonly feeds on these species, may be adapted to deal with this copious pollenkitt, but this need not impede its ability to digest pollens that lack such pollenkitt (e.g., *P.*

tanacetifolia). In contrast, the pollenkitt could be toxic to *O. lignaria* larvae or could interfere with digestion of nutrients. Comparative data are lacking, but studies suggest bees that use oily pollen are able to digest these oils or extract grain contents despite their presence (Suaréz-Cervera et al. 1994; Dobson and Peng 1997).

Specific signals from different pollen resources

Behavioral observations from *O. lignaria* and *O. californica* support the hypothesis that differences in specific cues are important in determining pollen collection by the adult. Bees' use of visual and olfactory cues to distinguish resources is well established (Von Frisch 1967; Menzel 1985; Pham-Delègue et al. 1987; Backhaus et al. 1993; Masson et al. 1993). My study shows that such cues not only differ among hosts, but also suggests that interpretation of cues might be context-dependent and differ among bee species. *Osmia californica* and *O. lignaria* continued to collect nectar from novel plant species when they were the only species available, but they would not collect pollen from them. Heliantheae pollen appeared to repel *O. lignaria*. Indeed females actively groomed after contacting it. Similar rejections of passively acquired pollen are reported for other bee species (e.g., Thomson 1986). Dobson (1987) posited that odors from the pollenkitt covering the grains play an important role in species-specific attraction; these and other chemicals might also deter some bee species, such as *O. lignaria,* from collecting pollen (e.g., Detzel and Wink 1993).

Phacelia tanacetifolia pollen did not repel *O. californica*; instead, pollen appeared to lack the requisite provisioning stimuli. Females readily collected *P. tanacetifolia* pollen in the presence of Heliantheae (their normal host), but ceased provisioning when presented *P. tanacetifolia* alone. One explanation is that *O. californica* received provisioning stimuli only from the Heliantheae plants. Alternatively, cues from *P. tanacetifolia* may have been interpreted as pollen-collection stimuli only in the presence of the normal host (that is, cues were context-dependent). A change in signal interpretation under different contexts, if true would have important implications for the evolution of pollen diet ranges. Such changes suggest that adding or dropping pollen species from the diet requires changes only in neurological processing of the signals.

Limits to novel pollen use for *O. californica*

Given that *O. californica* readily incorporated *P. tanacetifolia* into their provisions during controlled trials and larvae grew better on mixtures containing *P. tanacetifolia* than on pure Heliantheae pollen, why do natural populations of *O. californica* in northern Utah forego *Phacelia* and related Hydrophyllaceae pollen? Rather than using available *Phacelia* spp. and *Hydrophyllum capitatum* in the absence of Heliantheae bees used alternative Astera-

ceae. These Asteraceae may share host-recognition cues with Heliantheae and their availability precluded use of other species. I suggest two additional factors that could explain females' exclusion of Hydrophyllaceae from the pollen diet: foraging energetics and habitat selection.

Hydrophyllaceae pollen may not be economical to collect under most natural conditions. On the dates when *H. capitatum* was abundant, so was Heliantheae. During controlled experiments, *O. californica* appeared inefficient at collecting pollen from Hydrophyllaceae compared to Heliantheae. Females tamp their abdomens across the sunflower-like heads of Heliantheae to harvest pollen into the pollen-carrying hairs located there. They used similar movements to collect pollen from *P. tanacetifolia*, but they struggled to position themselves on the flowers and left visibly more pollen on anthers than did foraging *O. lignaria*. *Osmia lignaria* does not tamp when collecting pollen from *P. tanacetifolia*, but instead uses its legs to strip pollen from the anthers directly into the pollen-carrying hairs. Cripps and Rust (1989) suggested that the inability to glean pollen from non-composites might explain lack of use by *O. californica*. Behavioral inflexibility does not prohibit Hydrophyllaceae pollen collection, but it may make it unprofitable. *Osmia lignaria*, which favors Hydrophyllaceae, may further reduce profitability by depressing the availability of *H. capitatum* pollen.

Spatial separation of the two plant types in natural populations may also preclude collection of *H. capitatum.* Heliantheae typically grows on open hillsides, whereas *H. capitation* favors wooded areas (e.g., Williams and Tepedino 2002). Individual foraging bees show considerable site fidelity over multiple days (e.g., Heinrich 1976; Morse 1982; Thomson et al. 1982). If *O. californica* females began foraging in patches of abundant Heliantheae, they might not have sampled areas containing *H. capitatum*. Even if individuals did travel to Hydrophyllaceae patches, if these plants lack appropriate pollen collection stimuli bees would not have collected it.

Implications for specialization

This study, which examines the proximate factors affecting pollen use, complements the few existing phylogenetic studies that examine patterns of pollen use and specialization by bees (Müller 1996; Sipes and Wolf 2001). Such a phylogeny for *Osmia* would clarify interpretation of my results. For example, a topology with the specialist, *O. californica* in a derived position would support the conjecture, as shown for other herbivores, that adaptation to new hosts need not preclude use of ancestral host types. In contrast, a basal position for the specialist would indicate that shifts to novel pollens involve substantial loss in the ability to use previous hosts. Such phylogenetic grounding has expanded understanding of trophic specialization for a variety of herbivorous insects a (e.g., Funk 1998; Janz et al.2001).

Regardless of the polarity of pollen-use traits, my results suggest that specialists can remain labile in their ability to use alternative pollens, limited only by barriers at one life history stage. Such results are tantalizing, and call for comparisons of additional taxa from different lineages that could reveal the generality of this pattern for bees as appears to be the case for some other herbivores, e.g., butterflies (Thompson 1998; Janz et al. 2001). Additionally, manipulative experiments of flowers could identify floral characteristics that determine host use boundaries and might separate the roles that chemical, physical, or visual cues versus efficient foraging play in dictating dietary boundaries. For example, in the case of *Osmia,* would the presentation of *Phacelia* pollen on Asteraceae flowers allow for its use by *O. lignaria*? A positive result would suggest a defining role of pollen cues for pollen collection. If this same manipulation led to efficient harvest and preferential use by *O. californica,* an important role of foraging efficiency would be established. Whether for bees or other herbivores, wedding studies that determine the mechanistic basis underlying host use, (e.g., Roininen and Tahvanainen 1989) with phylogenetic estimates for the taxa involved may be one key to understanding the generality of processes underlying both the evolution and ecology of host use.

References

Alcock J (1995) Body size and its effect on male-male competition in the banksia bee, *Hylaeus alcyoneus* (Colletidae). J Insect Behav 8:149–159

Backhaus W, Oberwinkler J, Ehrlich I (1993) Minimal design of multiple color choice experiments with honey bees. In: Heisenberb M, Elsner N (eds) Proceedings of the 21st Gottingen Neurobiology Conference. Thieme, Gottingen, p 829

Beattie AJ (1971) A technique for the study of insect-borne pollen. Pan-Pac Entomol 47:82

Bernays EA (2001) Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. Annu Rev Entomol 46:703–727

Bernays EA, Minkenberg OPJM (1997) Insect herbivores: different reasons for being a generalist. Ecology 78:1157–1169

Bernays EA, Bright KL, Gonzalez N, Angel J (1994) Dietary mixing in a generalist herbivore: tests of two hypotheses. Ecology 75:1997–2006

Bullock SH et al. (1991) Nest provision and pollen foraging in three Mexican species of solitary bees (Hymenoptera: Apoidea). Pan-Pac Entomol 67:171–176

Cripps C, Rust RW (1989) Pollen preferences of seven *Osmia* species (Hymenoptera: Megachilidae). Environ Entomol 18:133–138

Cruden RW (1972) Pollination biology of *Nemophila menziezii* (Hydrophyllaceae) with comments on the evolution of oligolectic bees. Evolution 26:373–389

Detzel A, Wink M (1993) Attraction, deterrence or intoxication of bees (*Apis mellifera*) by plant allelochemicals. Chemoecology 4:8–18

Dobson HEM (1987) Role of flower and pollen aromas in host-plant recognition by solitary bees. Oecologia 72:618–623

Dobson HEM, Peng Y-S (1997) Digestion of pollen components by larvae of the flower-specialist bee *Chelostoma florisomne* (Hymenoptera: Megachilidae). J Insect Physiol 43:89–100

Erdtman G (1969) Handbook of palynology. Hafner, New York

Estes JR, Thorp RW (1975) Pollination ecology of *Pyrrhopappus carolinianus* (Compositae). Am J Bot 62:148–159

Fox CW, Nilsson JA, Mousseau TA (1997) The ecology of diet expansion in a seed-feeding beetle: pre-existing variation, rapid adaptation and maternal effects? Evol Ecol 11:183–194

Fry JA (1996) The evolution of host specialization: are trade-offs overrated? Am Nat 148S:S84-S107

Funk DJ (1998) Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. Evolution 52:1744–1759

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. Annu Rev Ecol Syst 19:207–233

Futuyma DJ, Wasserman SS (1981) Food plant specialization and feeding efficiency in the tent caterpillars *Malacosoma disstria* and *Malacosoma americanum*. Entomol Exp App 30:106–110

Heinrich B (1976) The foraging specializations of individual bumblebees. Ecol Monogr 46:105–128

Irwin RE, Brody AK, Waser NW (2001) The impact of flower larceny on individuals, populations, and communities. Oecologia 129:161–168

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:243–273

Janz N, Nyblom K, Nylin S (2001) Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. Evolution 55:783–796

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annu Rev Ecol Syst 29:83–112

Kim J (1997) Female size and fitness in the leaf-cutter bee *Megachile apicalis*. Ecol Entomol 22:275–282

Klostermeyer EC, Mech SJJ, Rasmussen WB (1973) Sex and weight of *Megachile rotundata* (Hymenoptera: Megachilidae) progeny associated with provisioning weights. J Kans Entomol Soc 46:536–548

Krombein KV (1967) Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian, Washington, D.C.

Levin MD, Haydak MH (1957) Comparative value of different pollens in the nutrition of *Osmia lignaria*. Bee World 9:221–226

Linsley EG (1958) The ecology of solitary bees. Hilgardia 27:543–599

Masson C et al. (1993) Recent advances in the concept of adaptation to natural odour signals in the honeybee, *Apis mellifera* L. Apidologie 24:169–194

Menzel R (1985) Learning in honey bees in an ecological and behavioral context. In: Hölldobler B, Lindauer M (eds) Experimental behavioral ecology and sociobiology. Thieme, Stuttgart, pp 55–74

Moran NA (1986) Benefits of host plant specificity in *Uroleucon* (Homoptera: Aphididae). Ecology 67:108–115

Morse DH (1982) Behavior and ecology of bumble bees. In: Hermann HR (ed) Social insects. Academic Press, New York, pp 245–322

Müller A (1996) Host-plant specialization in western palearctic Anthidiine bees (Hymenoptera: Apoidea: Megachilidae). Ecol Monogr 66:235–257

Parker FD, Tepedino VJ (1982) A nest and pollen-collection records of *Osmia sculleni* Sandhouse, a bee with hooked hairs on the mouthparts (Hymenoptera: Megachilidae). J Kans Entomol Soc 55:329–334

Pennings SC, Nadeau MT, Paul VJ (1993) Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. Ecology 74:879–890

Pham-Delègue MH, Etievant P, Masson C (1987) Molecular parameters involved in bee-plant relationships: a biological and chemical approach. Biochemie 69:661–670

Rau P (1937) The life history of *Osmia lignaria* and *O. cordata*, with notes on *O. conjuncta*. Annu Entomol Soc Am 39:324–342

Roininen H, Tahvanainen J (1989) Host selection and larval performance of two willow-feeding sawflies. Ecology 70:129–136

Roulston TH, Cane JH, Buchmann SL (2000) What governs the protein content of pollen grains: pollinator preferences, pollen-pistil interactions, or phylogeny? Ecol Monogr 70:617–643

Rust RW (1974) The systematics and biology of the genus *Osmia*, subgenera *Osmia, Chalcosmia*, and *Cephalosmia* (Hymenoptera: Megachilidae). Wasmann J Biol 32:1–93

Singer MC (1983) Determinants of multiple host use by a phytophgous insect population. Evolution 37:389–403

Singer MC, Ng D, Thomas CD (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. Evolution 42:977–985

Sipes S, Wolf PG (2001) Phylogenetic relationships within Diadasia, a group of specialist bees. Mol Phylogenet Evol 19:144–156

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Stanley RG, Linskens HF (1974) Pollen biology, biochemistry, and management. Springer, Berlin Heidelberg New York

Strickler K (1979) Specialization and foraging efficiency of solitary bees. Ecology 60:998–1009

Suaréz-Cervera M, Marquez J, Bosch J, Seoane-Camba J (1994) An ultrastructural study of pollen grains consumed by larvae of *Osmia* bees (Hymenoptera, Megachilidae). Grana 33:191–204

Sugiura N, Maeta Y (1989) Parental investment and offspring sex ratio in a solitary mason bee, *Osmia cornifrons* (Radoszkowski)(Hymenoptera, Megachilidae). Jpn J Entomol 57:861–875

Tepedino VJ, Torchio PF (1982) Phenotypic variability in nesting success among *Osmia lignaria propinqua* females in a glasshouse environment (Hymenoptera: Megachilidae). Ecol Entomol 7:453–462

Thomas CD, Ng D, Singer MC, Mallet JLB, Parmesan C, Billington HL (1987) Incorporation of a European weed into the diet of a North American herbivore. Evolution 41:892–901

Thompson JN (1988) Evolutionary genetics of oviposition preference in swallowtail butterflies. Evolution 42:118–128

Thompson JN (1993) Preference hierarchies and the origin of geographic specialization in host use in swallowtail butterflies. Evolution 47:1585–1594

Thompson JN (1994) The coevolutionary process. University of Chicago Press, Chicago

Thompson JN (1996) Trade-offs in larval performance on normal and novel hosts. Entomol Exp Appl 80:133–139

Thompson JN (1998) The evolution of diet breadth: monophagy and polyphagy in swallowtail butterflies. J Evol Biol 11:563–578

Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. Annu Rev Entomol 36:65–89

Thomson JD (1986) Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. J Ecol 74:329–341

Thomson JD, Thomson BA (1992) Pollen presentation and viability schedules in animal-pollinated plant: consequences for reproductive success. In: Wyatt R (ed) Ecology and evolution of plant reproduction. Chapman and Hall, New York, pp 1–24

Thomson JD, Maddison WP, Plowright RC (1982) Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). Oecologia 54:326–336

Thorp RW (1969) Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). University of California Press, Berkeley

Thorp RW (1979) Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann Mo Bot Gard 66:788–812

Torchio PF (1976) Use of *Osmia lignaria* Say (Hymenoptera: Apoidea, Megachilidae) as a pollinator in an apple and prune orchard. J Kans Entomol Soc 49:475–482

Torchio PF (1985) Field experiments with *Osmia lignaria propinqua* Cresson, in apple orchards: V (1979–1980) methods of introducing bees, nesting success, seed counts, fruit yields (Hymenoptera: Megachilidae). J Kans Entomol Soc 58:448—464

Torchio PF (1989) In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). Ann Entomol Soc Am 82:599–615

Torchio PF, Tepedino VJ (1982) Parsivoltinism in three species of *Osmia* bees. Psyche 89:221–238

Via S (1990) Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. Annu Rev Entomol 35:421–446

Visscher PK, Danforth BN (1993) Biology of *Calliopsis pugionis* (Hymenoptera: Andrenidae): nesting, foraging, and investment sex ratio. Ann Entomol Soc Am 86:822–832

Von Frisch K (1967) The dance language and orientation of bees. Belknap, Cambridge

Williams NM, Tepedino VJ (2003) Balancing resource distribution and nutrient demands: foraging decisions of a solitary mason bee *Osmia lignaria*. Behav Ecol (in press)