Natural History Note

Asteraceae Pollen Provisions Protect *Osmia* Mason Bees (Hymenoptera: Megachilidae) from Brood Parasitism

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abstract: Many specialist herbivores eat foods that are apparently low quality. The compensatory benefits of a poor diet may include protection from natural enemies. Several bee lineages specialize on pollen of the plant family Asteraceae, which is known to be a poor-quality food. Here we tested the hypothesis that specialization on Asteraceae pollen protects bees from parasitism. We compared rates of brood parasitism by *Sapyga* wasps on Asteraceae-specialist, Fabeae-specialist, and other species of *Osmia* bees in the field over several years and sites and found that Asteraceae-specialist species were parasitized significantly less frequently than other species. We then tested the effect of Asteraceae pollen on parasites by raising *Sapyga* larvae on three pollen mixtures: Asteraceae, Fabeae, and generalist (a mix of primarily non-Asteraceae pollens). Survival of parasite larvae was significantly reduced on Asteraceae provisions. Our results suggest that specialization on low-quality pollen may evolve because it helps protect bees from natural enemies.

Keywords: cleptoparasites, specialization, tritrophic interactions, oligolecty, Sapygidae.

Introduction

Many animals choose to eat seemingly poor-quality or unpalatable foods (e.g., Freeland and Janzen 1974; Berenbaum 1990). Numerous herbivores have evolved preferences for plants rich in secondary metabolites that would harm nonspecialists (Ehrlich and Raven 1964; Berenbaum 1990). Some adult insects preferentially oviposit on certain food plants even if their larvae could develop as well—or better—on other hosts (Smiley 1978; Bernays and Graham 1988). This apparently paradoxical phenomenon suggests that dietary specialization has evolved for reasons other than the nutritional needs of the insect. One hypothesis suggests that indirect benefits outweigh the direct fitness costs of consuming poor-quality food. For example, toxic secondary metabolites in nectar can reduce pathogen load in bumblebees (Manson et al. 2010). Dietary specialists may also suffer less mortality from generalist predators (Bernays and Graham 1988; Bernays and Cornelius 1989; Wcislo and Cane 1996; Singer et al. 2014), in part because compounds sequestered from their food are harmful to prospective predators (Pasteels et al. 1983; Dyer 1995).

Many bee species are oligolectic, collecting pollen from only a few related plant species (Wcislo and Cane 1996). The plant family Asteraceae is well represented among the host plants of oligolectic bees, with specialization on Asteraceae pollen having arisen in multiple bee lineages (Moldenke 1979; Hurd et al. 1980; Müller 1996; Müller and Kuhlmann 2008; Praz et al. 2008). Interestingly, bees that are not Asteraceae specialists seem to develop poorly—and frequently die—when fed only Asteraceae pollen (Levin and Haydak 1957; Guirguis and Brindley 1974; Williams 2003; Tasei and Aupinel 2008). Even Asteraceae-specialist bees may be harmed by a pure Asteraceae pollen diet: development time can be prolonged (Williams 2003; Praz et al. 2008) and growth can be stunted (Williams 2003) when larvae are fed Asteraceae pollen alone instead of a mixed diet.

Here we propose a novel application of the hypothesis that consumption of unpalatable food can indirectly increase fitness. We suggest that the repeated evolution of specialization on Asteraceae pollen may have occurred because Asteraceae pollen serves an antiparasite function, conferring enemy-free space (Lawton 1978) for bees able to use it, similar to the way that toxic food plants can indirectly benefit their insect herbivores. Brood parasitism (called cleptoparasitism) is common among solitary bees (Michener 2000). Cleptoparasites oviposit into nest cells, where the parasite larva kills the host egg and consumes its pollen and nectar provisions. Sapygid wasps are common cleptoparasites of bees in the family Megachilidae (Torchio 1972, 1979; Münster-Swendsen and Calabuig 2000; Goodell 2003), causing mortality rates of up to

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56% in our study populations. However, in our field observations, we have never found nests of Asteraceae specialists parasitized by sapygid wasps, and we know of no records of sapygid wasps parasitizing Asteraceae specialists. Furthermore, we have observed nest-searching female sapygids approach and apparently reject the nests of Asteraceae-specialist bees (S. Silverman, personal observation). These observations led us to hypothesize that sapygid wasps—generalists that attack several bee species—may be unable to tolerate Asteraceae pollen.

We tested this hypothesis with both an observational and an experimental study. First we determined whether Asteraceae specialists experience lower rates of sapygid parasitism than other related bees over 4 years of observation. We then tested our hypothesis experimentally by forcing larval wasps to feed on different pollens and comparing their survival and development on Asteraceae and non-Asteraceae pollen provisions.

Methods

Study System

Trap nests for cavity-nesting bees (wood blocks with drilled holes lined with paper straws) were established in 2008, 2013, 2014, and 2015 at several sites around the Rocky Mountain Biological Laboratory, Crested Butte, Colorado (table A1; tables A1–A3 and figure A1 are available online). Trap nest occupants included *Osmia* (*Hapsidosmia*) *iridis*, which specializes on pollen of the legume tribe Fabeae (J. R. K. Forrest, unpublished data); *Osmia* (*Melanosmia*) *tristella* and *Osmia* (*Melanosmia*) *tersula*, both pollen generalists; and *Osmia* (*Helicosmia*) *coloradensis*, *Osmia* (*Cephalosmia*) *montana*, and *Osmia* (*Cephalosmia*) *subaustralis*, all of which specialize on pollen of the family Asteraceae. The most common nest parasites of *Osmia* spp. across our study sites were *Sapyga* spp. (primarily *Sapyga pumila*, based on previous work in this area; Forrest and Thomson 2011), which were found in 14% of all nest cells, but we occasionally observed parasitism by *Stelis* spp. and parasitoid wasps (each <1% of nest cells).

Incidence of Parasitism

The occupants of *Osmia* nests constructed in 2008 were allowed to emerge into emergence traps over the subsequent two summers (Forrest and Thomson 2011), and the emerged specimens were used to determine rates of sapygid parasitism on each species of nesting bee. Pollen contents of nests were not examined in 2008, so pollen types were inferred based on known host bee preferences, as listed above. In some cases, all cells of a nest were parasitized, so the host taxon could not be determined; these nests were excluded from analysis. We also excluded from analysis all nests of *Osmia pikei*, a generalist species that is active earlier than *Sapyga* in the season (mid-May–mid-June vs. mid-June–late July). Nesting periods of all other *Osmia* species at our study sites overlap with the activity period of *Sapyga*.

In the summers of 2013–2015, pollen samples were taken from the innermost and outermost cells of each completed nest (or only the innermost cell if the nest contained less than four cells) using clean forceps to confirm that bees did not change pollen usage over the course of nest construction. Pollen samples were melted on a slide with fuchsin stain (Kearns and Inouye 1993) and examined under a compound microscope at ×200–400 magnification by two independent observers with access to a local pollen reference library and a list of plants in flower at the site during nest construction. Each pollen type in the sample was identified at least to family (frequently to genus). Nests were considered "specialist" Fabeae or Asteraceae nests if that taxon comprised ≥95% of the total pollen biovolume. All other nests were considered "various" for the purpose of this study; various nests sometimes contained a single dominant pollen type (e.g., Rosaceae, *Penstemon*).

To determine parasitism rates on trap nest occupants other than *O. montana* and *O. subaustralis*, we cut a window (imperceptible to the host bee) into the paper-straw wall of each completed nest cell to check for parasites. For nests of the latter two species, which bury their eggs in a pollen mass that fills virtually the entire nest cell (Torchio 1989), visual inspection for parasites was impossible. For these species, we determined parasitism rates after adult emergence (as for all 2008 nests).

Wasp Development

Sapyga eggs were collected from parasitized *Osmia* nest cells in 2014 and 2015. Host nest pollen type was determined for most of the collected wasps using the methods described above. All eggs were placed into gelatin capsules, with pollen provisions collected from *Osmia* nests in 2013, 2014, or 2015 or in one case, with pollen collected directly from flowers of *Wyethia amplexicaulis* (Asteraceae). Most provisions thus contained bee regurgitate and nectar (but no bee egg) in addition to pollen. Wasps were haphazardly assigned to three pollen provision treatments: pure (i.e., ≥95%) Fabeae pollen ($N = 21$), generalist pollen (a mixture of primarily non-Asteraceae pollens obtained from several different nests; $N = 17$), or pure (≥95%) Asteraceae pollen ($N = 30$; table A2). The pollen in each provision was identified as described above. Pollen provisions from 2013 and 2014 were stored over winter at 0°C before use in 2014 or 2015. Additional pollen provisions were collected and used in the same year (2014 or 2015); these were also kept cold until use. To ensure that the crumbly Asteraceae pollen did not shift and crush the wasp eggs, a small amount of commercial honey

was spread over the base of all capsules (regardless of pollen type) before placing pollen and wasps inside.

Wasps were kept inside their capsules in an incubator at room temperature (18°–25°C) during summer 2014 and at ~18°C during summer 2015 and checked daily. We noted dates of hatching, defecation (an indication of reaching last instar; see Torchio 1972), cocoon spinning, and/or death. Cocoon completion (2014) or the end of daily observations (August 2015) was the end point for survival analyses.

Data Analysis

Analyses were performed in R, version 3.2.2 (R Core Team 2015). To test whether incidence of parasitism varied with respect to host bee pollen type (Asteraceae, Fabeae, or various), while accounting for site and year effects, we attempted to use generalized linear mixed models. Because there were no parasitized Asteraceae pollen nests, these models failed to converge. We therefore instead conducted a Kruskal-Wallis test on the proportion of nests parasitized by *Sapyga* as a function of pollen type, treating as independent replicates each of the 14 site/year combinations in which both parasites and Asteraceae-specialist bees occurred.

To analyze survival differences, we used the Kaplan-Meier estimator (Kaplan and Meier 1958) and conducted log-rank tests using the R package survival (Therneau 2014). Too few wasps reached the defecation ($N = 9$) or cocoon-spinning ($N = 3$) stage to analyze development differences. We first tested for effects of study year (2014 or 2015) or pollen age (pollen collected the same year as the study or the previous year) on wasp larvae survival. We also tested whether wasp survival differed according to whether wasps were placed on a pollen provision of the same or a different type as their original host nest. For this comparison, we tested only wasps placed on Fabeae or generalist pollen provisions, because no wasps were collected from Asteraceae provisions. Because there was no difference in wasp survival in any of these tests (all $P > .15$), we combined all data to test for differences in survival of wasps raised on the different provision types. The parasite incidence data and the experimental data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.4sd09 (Spear et al. 2016).

Results

We collected parasitism incidence data on 631 *Osmia* nests (fig. 1). None of the 72 nests of Asteraceae specialists was parasitized by *Sapyga*, while the sapygid parasitism rate on other pollen types combined was 33%. The frequency of parasitized nests differed significantly among the three pollen types (Kruskal-Wallis $\chi^2 = 21.8$, df $= 2$, $P < .0001$). This difference remained significant if we excluded the 2008 data as well as all data on *Osmia montana* and *Osmia subaustralis*, for which parasitism rates were reconstructed from emerged (i.e., successfully matured) insects rather than from dissection of newly completed nests (Kruskal-Wallis $\chi^2 = 16.4$, df $= 2$, $P < .001$).

In our experiments, we reared 68 sapygid wasp larvae in total (22 in 2014, 46 in 2015; fig. 2). Wasps were collected from generalist and non-Asteraceae specialist (primarily Fabeae-specialist) *Osmia* nests (table A3). Larval wasp survival differed significantly among the three provision types (Kaplan-Meier analysis, log-rank test, $\chi^2 = 26$, df $= 2$, $P < .0001$, $N = 68$; fig. 3). Specifically, wasps raised on Asteraceae provisions were more likely to die than those raised on generalist ($\chi^2 = 13.1$, df $= 1$, $P < .001$, $N = 47$) or Fabeae ($\chi^2 = 21.5$, df $= 1$, $P < .0001$, $N = 51$) provisions. These results are qualitatively unchanged if the wasp reared on pure Asteraceae pollen, rather than nest provisions, is excluded from analysis. Survival did not differ between Fabeae and generalist provisions ($\chi^2 = 0.3$, df $= 1$, $P = .595$, $N = 38$; fig. 3). Of nine wasps that reached the defecation stage, only one was raised on Asteraceae provisions (fig. 2). Of the three wasps that reached the cocoon-spinning stage, one was raised on generalist provisions, two on Fabeae provisions, and none on Asteraceae provisions.

Discussion

This study demonstrates that specialization on Asteraceae pollen can protect mason bees from brood parasitism by sapygid wasps. In the field, *Osmia* species that specialize on Asteraceae pollen were parasitized significantly less frequently than Fabeae specialists or generalists. In addition, the sapygid wasps in our experiment, like many generalist bees (Müller and Kuhlmann 2008 and references therein), seemed unable to develop to maturity on a diet of Asteraceae pollen. Sapygids reared on Asteraceae pollen provisions died sooner than those fed Fabeae or generalist pollen provisions. Our study therefore provides evidence that Asteraceae specialization can deter sapygid wasps from ovipositing into specialist nests, likely because wasp larvae cannot grow to adulthood on a diet of Asteraceae pollen.

Although *Sapyga* survival was significantly reduced on Asteraceae pollen compared to the other tested pollens, survival was low in all treatments compared with survival of wasps allowed to develop in the field (J. R. K. Forrest, personal observation). There may be several reasons for the low overall survival, including handling of the delicate eggs (many other eggs died in transfer and could not be used in the experiment), the absence of a host egg in the experimental pollen provisions, or the addition of honey to the provisions. We note that the two latter differences from natural conditions would have resulted in lower relative protein content in the provisions, which may have impaired larval devel-

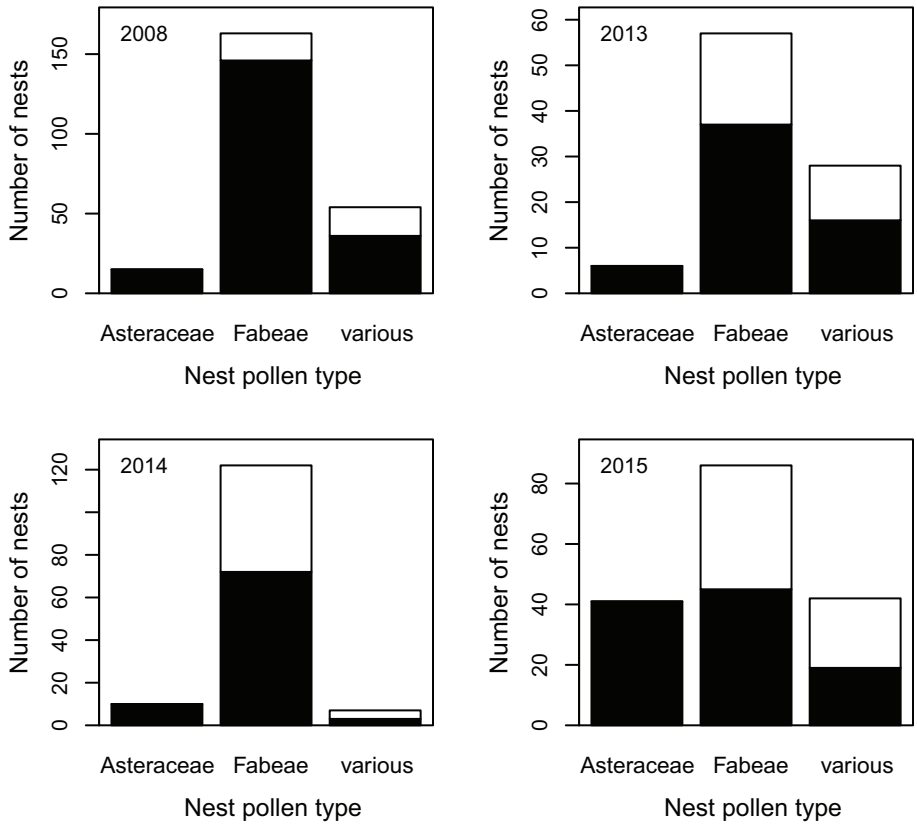


Figure 1: Incidence of parasitism by *Sapyga* in *Osmia* nests, 2008–2015. Filled portions of bars represent unparasitized nests; unfilled portions represent parasitized nests (i.e., nests in which at least one cell contained a *Sapyga* egg [2013–2015] or yielded an emerging adult *Sapyga* [2008]). Pollen contents were inferred for 2008 nests based on the host species and were determined by taking pollen samples from nests in 2013–2015. Various = all nests not dominated by Asteraceae or Fabeae pollen (see table A3, available online).

opment. (Low protein content in larval food is known to reduce final body size in some bees, for example [Roulston and Cane 2002].)

Floral specialization has previously been proposed as a means for bees to obtain enemy-free space, since certain parasites are acquired at flowers and may be avoided by restricting foraging to certain plant species (Wcislo and Cane 1996). In addition, honeybees (*Apis mellifera*) are known to occasionally collect certain plant resins, nectars, and pollens to self-medicate against pathogens (Simone-Finstrom and Spivak 2012; Gherman et al. 2014), and feeding bumblebees a diet of alkaloid-rich nectar can reduce gut pathogen load (Manson et al. 2010). To our knowledge, however, it has not previously been suggested that species-level specialization on a restricted set of pollens for larval development (oligolecty) might be the result of selection imposed by parasites.

Because sapygids in our study were able to develop when fed pure Fabeae pollen provisions, we cannot conclude that pollen specialization in general serves an antiparasite function. Fabaceae is a popular host family for oligolectic bees, yet some Fabaceae specialists are frequently parasitized (Müller 1996)—as we observed here. The *Ranunculus*-specialist bee *Chelostoma florisomne* is also attacked by sapygids (Münster-Swendsen and Calabuig 2000), despite the fact that *Ranunculus* pollen is apparently inadequate for development of nonspecialist bees (Praz et al. 2008). For unknown reasons, specialization on Asteraceae pollen seems necessary to prevent sapygid parasitism—similar to the way specialization on certain toxic host plants can benefit other insect herbivores.

It is unclear why Asteraceae pollen is unsuitable as a sole protein source for most bee species. Several Asteraceae pollens are known to have low protein content, but this seems not to be the only reason for the inadequacy of Asteraceae pollen (Tasei and Aupinel 2008); rather, it may lack essential amino acids or contain toxins (Levin and Haydak 1957; Roulston and Cane 2000; Müller and Kuhlmann 2008; Praz et al. 2008; Tasei and Aupinel 2008). Further study is required to distinguish among these possibilities. For instance, experimental protein additions to Asteraceae provisions might be

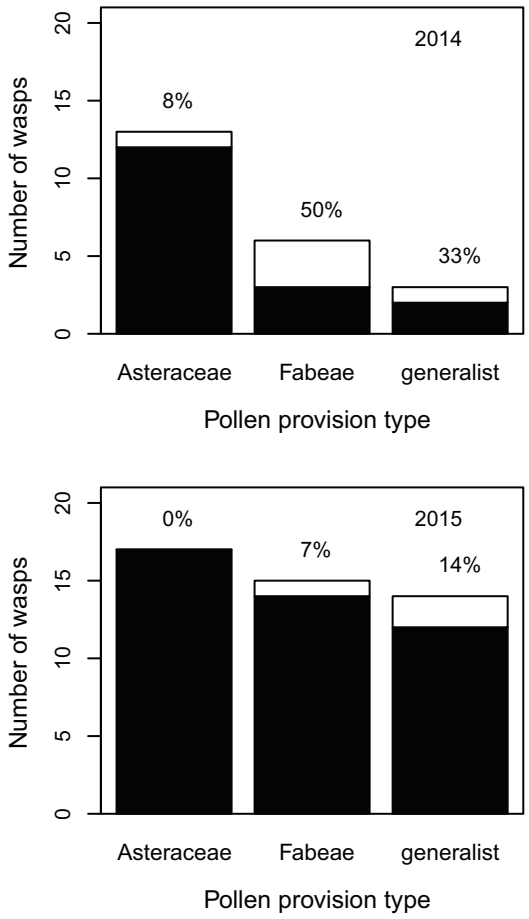


Figure 2: Numbers of sapygid wasps used in experiments in each year. Unfilled portions of bars represent wasps surviving to the defecation stage; filled portions represent those not surviving to defecation. Percentages surviving to defecation are indicated above each bar.

used to rule out protein deficiency as a mechanism, while expression of detoxification genes in response to different diets might be used to evaluate toxicity (e.g., Mao et al. 2013). It is also essential to note that we cannot separate effects of the pollen itself from effects of bee regurgitate, which was present in most pollen provisions. However, Asteraceae provisions used in our experiment came from two species (*Osmia coloradensis* and *Osmia montana*; *Osmia subaustralis* provisions were not available), representing two subgenera and likely two origins of Asteraceae specialization (see phylogeny of Rightmyer et al. 2013), and survival of wasps raised on these two provision types did not differ (fig. A1; Kaplan-Meier analysis, log-rank test, $\chi^2 = 1.0$, df $= 1$, $N = 23$, $P = .316$). Hence, the negative effects of Asteraceae provisions cannot be attributed to a single species' regurgitate. In any case, it seems clear that Asteraceae-specialist provisions reduce sapygid wasp survival and that *Sapyga* avoid ovipositing in Asteraceae-specialist nests.

Nevertheless, small amounts of Asteraceae pollen may be manageable for sapygids. Some of the generalist pollen mixtures used in our experiment contained some Asteraceae pollen, and a wasp from one such nest lived through several instars. Furthermore, many generalist bees are known to collect small amounts of Asteraceae pollen (Müller 1996). We therefore suspect that specialization on Asteraceae pollen is necessary for bees to obtain protection from sapygid parasitism; however, further study of the dosage dependence of Asteraceae pollen toxicity would be required to test this.

Regardless of the mechanism, the inability of sapygid wasps to use pure Asteraceae pollen and their avoidance of Asteraceae-specialist nests for oviposition could be a strong fitness advantage for Asteraceae-specialist bees. This advantage could have favored the evolution of specialization on these plants despite the detrimental effects of feeding exclusively on apparently low-quality pollens (Williams 2003; Müller and Kuhlmann 2008; Praz et al. 2008). However, sapygids, which attack only certain bee families, cannot be the sole agents responsible for the evolution of Asteraceae specialization in many bee lineages. The ability to exploit a pollen source that many bees cannot use should also reduce competition for resources, providing additional selective pressure for specialization. In addition, Asteraceae pollen may have more broadly toxic (e.g., antimicrobial) properties, similar to alkaloid-rich nectar (Manson et al. 2010)—a possibility that remains to be investigated. If so, the indirect fitness benefits of exploiting toxic pollen could help explain the multiple origins of Asteraceae specialization in bees.

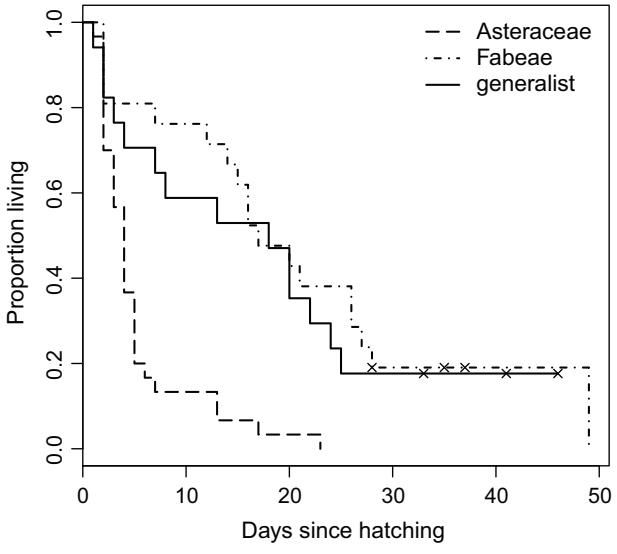


Figure 3: Kaplan-Meier survival curves for wasps raised on Asteraceae ($N = 30$), generalist ($N = 17$), or Fabeae ($N = 21$) pollen provisions. Data are censored at cocoon completion for 2014 wasps or at the end of observations for 2015 wasps (× symbol on curves).

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A female *Sapyga* wasp at an experimental nesting block, watching an *Osmia* nest entrance for an opportunity to oviposit. Photo credit: Jessica R. K. Forrest.