

Asteraceae pollen provisions protect *Osmia* mason bees (Hymenoptera: Megachilidae) from brood parasitism

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Online Appendix A: Information about sapygid wasp larvae and pollen types used in experiment.

Includes Table A1, Table A2, Table A3, and Figure A1

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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, Fabaceae-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, Fabaceae, 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.

Introduction

Many animals choose to eat seemingly poor-quality or unpalatable foods (e.g., Freeland & Janzen 1974; Berenbaum 1990). Numerous herbivores have evolved preferences for plants rich in secondary metabolites that would harm non-specialists (Ehrlich & 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 & 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, Otterstatter & Thomson 2010). Dietary specialists may also suffer less mortality from generalist predators (Bernays & Graham 1988; Bernays & Cornelius 1989; Wcislo & Cane 1996; Singer et al. 2014), in part because compounds sequestered from their food are harmful to prospective predators (Pasteels, Grégoire & Rowell-Rahier 1983; Dyer 1995).

Many bee species are oligolectic, collecting pollen from only a few related plant species (Wcislo & 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, LaBerge & Linsley 1980; Müller 1996; Müller & Kuhlmann 2008; Praz, Müller & Dorn 2008). Interestingly, bees that are not Asteraceae specialists seem to develop poorly—and frequently die—when fed only Asteraceae pollen (Levin & Haydak 1957; Guirguis & Brindley 1974; Williams 2003; Tasei & 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 anti-parasite 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; Torchio 1979; Münster-Swendsen & Calabuig 2000; Goodell 2003), causing mortality rates of up to 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.

Here, we test this hypothesis with both an observational and an experimental study. First, we determine whether Asteraceae specialists experience lower rates of sapygid parasitism than other related bees, over four years of observation. We then test 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, Colorado, USA (online appendix A, table A1). Trap-nest occupants included *Osmia* (*Hapsidosmia*) *iridis*, which specializes on pollen of the legume tribe Fabaeae (J. Forrest, unpublished data); *O.* (*Melanosmia*) *tristella* and *O.* (*Melanosmia*) *tersula*, both pollen generalists; and *O.* (*Helicosmia*) *coloradensis*, *O.* (*Cephalosmia*) *montana*, and *O.* (*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 & 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 *O. pikei*, a generalist species that is active earlier in the season than *Sapyga*

(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 <4 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 & 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” Fabaceae or Asteraceae nests if that taxon comprised $\geq 95\%$ 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., $\geq 95\%$) Fabaceae pollen ($N = 21$), “generalist” pollen (a mixture of primarily non-Asteraceae pollens obtained from several different nests; $N = 17$), or pure ($\geq 95\%$) 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 ($18\text{--}25^{\circ}\text{C}$) during summer 2014 and at $\sim 18^{\circ}\text{C}$ 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 endpoint 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, Fabae, or “various”), while accounting for site and year effects, we attempted to use generalized linear mixed models.

Because there were zero 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 & Meier 1958) and conducted log-rank tests using the R package survival (Therneau 2014). Too few wasps reached defecation ($N = 9$) or cocoon-spinning stage ($N = 3$) 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 Fabae 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 $P > 0.15$), 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, Silverman & Forrest 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 $\chi^2 = 21.8$, $df = 2$, $P < 0.0001$). This difference remained significant if we excluded the 2008 data as well as all data on *O. montana* and *O. subaustralis*, for which parasitism rates were reconstructed from emerged (i.e., successfully matured) insects rather than from dissection of newly completed nests (Kruskal-Wallis $\chi^2 = 16.4$, $df = 2$, $P < 0.001$).

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 Fabae-specialist) *Osmia* nests (table A3). Larval wasp survival differed significantly among the three provision types (Kaplan-Meier analysis, log-rank test, $\chi^2 = 26$, $df = 2$, $P < 0.0001$, $N = 68$; fig. 3). Specifically, wasps raised on Asteraceae provisions were more likely to die than those raised on generalist ($\chi^2 = 13.1$, $df = 1$, $P < 0.001$, $N = 47$) or Fabae provisions ($\chi^2 = 21.5$, $df = 1$, $P < 0.0001$, $N = 51$). 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 Fabae and generalist provisions ($\chi^2 = 0.3$, $df = 1$, $P = 0.595$, $N = 38$; fig. 3). Of nine wasps that reached defecation stage, only one was raised on Asteraceae provisions (fig. 2). Of the three wasps that reached cocoon-spinning stage, one was raised on generalist provisions, two on Fabae 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 Fabaceae specialists or generalists. In addition, the sapygid wasps in our experiment, like many generalist bees (Müller & Kuhlmann 2008 and references cited therein), seemed unable to develop to maturity on a diet of Asteraceae pollen. Sapygids reared on Asteraceae pollen provisions died sooner than those fed Fabaceae 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. 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 development. (Low protein content in larval food is known to reduce final body size in some bees, for example (Roulston & 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 & Cane 1996). In addition, honeybees (*Apis mellifera*) are

known to occasionally collect certain plant resins, nectars, and pollens in order to “self-medicate” against pathogens (Simone-Finstrom & 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 Fabaceae pollen provisions, we cannot conclude that pollen specialization, in general, serves an anti-parasite function. Fabaceae is a popular host-group 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 & Calabuig 2000), despite the fact that *Ranunculus* pollen is apparently inadequate for development of non-specialist 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 & Aupinel 2008); rather, it may lack essential amino acids or contain toxins (Levin & Haydak 1957; Roulston & Cane 2000; Müller & Kuhlmann 2008; Praz et al. 2008; Tasei & Aupinel 2008). Further study is required to distinguish among these possibilities. For instance, experimental protein additions to Asteraceae provisions might be 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, Schuler & Berenbaum 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 (*O. coloradensis* and *O. montana*; *O. subaustralis* provisions were not available), representing two subgenera and likely two origins of Asteraceae specialization (see phylogeny of Rightmyer, Griswold & Brady 2013), and survival of wasps raised on these two provision types did not differ (fig. A1; Kaplan-Meier analysis, log-rank test, $\chi^2 = 1.0$, $df = 1$, $N = 23$, $P = 0.316$). 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 & Kuhlmann 2008; Praz et al. 2008). However, sapygids, which only attack 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., anti-microbial) 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.

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Online Appendix A

Information about sapygid wasp larvae and pollen types used in experiment.

Table A1. Collection sites for sapygids used in experiment.

Site name	Latitude (N)	Longitude (W)	Elevation (m)
Brush Creek	38° 51' 39.4"	106° 55' 10.6"	2730
South Gothic	38° 57' 0.0"	106° 58' 42.0"	2859
Mt. Crested Butte	38° 53' 19.4"	106° 57' 43.3"	2869
Rosy Point	38° 55' 58.0"	106° 58' 7.3"	2879
Kebler Clearing	38° 51' 30.9"	107° 3' 37.6"	2956
401 Trail	38° 58' 14.8"	106° 59' 26.0"	3020
Kebler Pass	38° 51' 8.8"	107° 6' 3.9"	3040
Virginia Basin	38° 58' 37.1"	106° 58' 34.3"	3440

Table A2. Constituent plant genera for each pollen type used for rearing sapygid wasp larvae. Each pollen provision of a given type included some subset of the genera listed here. Generalist provisions included at least two of the listed genera, from different families.

Asteraceae	generalist	Fabeae
<i>Erigeron</i> (Asteraceae)	<i>Agastache</i> (Lamiaceae)	<i>Lathyrus</i> (Fabaceae)
<i>Helianthella</i> (Asteraceae)	<i>Arctostaphylos</i> (Ericaceae)	<i>Vicia</i> (Fabaceae)
<i>Heliomeris</i> (Asteraceae)	<i>Hackelia</i> (Boraginaceae)	
<i>Heterotheca</i> (Asteraceae)	<i>Helianthella</i> (Asteraceae)	
<i>Hymenoxys</i> (Asteraceae)	<i>Hydrophyllum</i> (Boraginaceae)	
<i>Wyethia</i> (Asteraceae)	<i>Lupinus</i> (Fabaceae)	
	<i>Mertensia</i> (Boraginaceae)	
	<i>Penstemon</i> (Plantaginaceae)	
	<i>Phacelia</i> (Boraginaceae)	
	<i>Potentilla</i> (Rosaceae)	
	<i>Viola</i> (Violaceae)	

Table A3. Host nest pollen type of sapygid wasps used in experiment. “Generalist” refers to nests that included at least two pollen types, each making up >25% of the nest contents. Other nests were dominated by the listed pollen type, with no other pollen making up more than 25% of the nest contents.

Host nest pollen type	Number of wasps 2014	Number of wasps 2015
<i>Arctostaphylos</i>	0	2
Asteraceae	0	0
Fabeae	17	36
<i>Lupinus</i>	0	1
<i>Penstemon</i>	1	4
Rosaceae	0	3
generalist	2	1
unknown	2	0

Literature Cited

- Berenbaum, M.R. (1990) Evolution of specialization in insect-umbellifer associations. *Annual Review of Entomology*, **35**, 319-343.
- Bernays, E.A. & Cornelius, M.L. (1989) Generalist caterpillar prey are more palatable than specialists for the generalist predator *Iridomyrmex humilis*. *Oecologia*, **79**, 427-430.
- Bernays, E.A. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology*, **69**, 886-892.
- Dyer, L.A. (1995) Tasty generalists and nasty specialists? Antipredator mechanisms in tropical lepidopteran larvae. *Ecology*, **76**, 1483-1496.
- Ehrlich, P.R. & Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution*, **18**, 586-608.
- Forrest, J.R.K. & Thomson, J.D. (2011) An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs*, **81**, 469-491.
- Freeland, W.J. & Janzen, D.H. (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist*, **108**, 269-289.
- Gherman, B., Denner, A., Bobiș, O., Dezmirean, D., Mărghitaș, L., Schlüns, H., Moritz, R.A. & Erler, S. (2014) Pathogen-associated self-medication behavior in the honeybee *Apis mellifera*. *Behavioral Ecology and Sociobiology*, **68**, 1777-1784.
- Goodell, K. (2003) Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia*, **134**, 518-527.
- Guirguis, G.N. & Brindley, W.A. (1974) Insecticide susceptibility and response to selected pollens of larval alfalfa leafcutting bees, *Megachile pacifica* (Panzer) (Hymenoptera: Megachilidae). *Environmental Entomology*, **3**, 691-694.
- Hurd, P.D., LaBerge, W.E. & Linsley, E.G. (1980) Principal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions in Zoology*, **310**, 1-158.
- Kaplan, E. & Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association*, **53**, 457-481.
- Kearns, C.A. & Inouye, D.W. (1993) *Techniques for Pollination Biologists*. University Press of Colorado, Niwot, Colorado, USA.
- Lawton, J.H. (1978) Host-plant influences on insect diversity: the effects of space and time. *Diversity of Insect Faunas* (eds L.A. Mound & N. Waloff), pp. 105-125. Blackwell Scientific, Oxford, UK.

- Levin, M.D. & Haydak, M.H. (1957) Comparative value of different pollens in the nutrition of *Osmia lignaria*. *Bee World*, **38**, 221-226.
- Manson, J.S., Otterstatter, M.C. & Thomson, J.D. (2010) Consumption of a nectar alkaloid reduces pathogen load in bumble bees. *Oecologia*, **162**, 81-89.
- Mao, W., Schuler, M.A. & Berenbaum, M.R. (2013) Honey constituents up-regulate detoxification and immunity genes in the western honey bee *Apis mellifera*. *Proceedings of the National Academy of Sciences of the USA*, **110**, 8842-8846.
- Michener, C.D. (2000) *Bees of the World*. Johns Hopkins University Press, Baltimore, MD, USA.
- Moldenke, A.R. (1979) Host-plant coevolution and the diversity of bees in relation to the flora of North America. *Phytologia*, **43**, 357-419.
- Müller, A. (1996) Host-plant specialization in western Palearctic anthidiine bees (Hymenoptera: Apoidea: Megachilidae). *Ecological Monographs*, **66**, 235-257.
- Müller, A. & Kuhlmann, M. (2008) Pollen hosts of western palaeartic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biological Journal of the Linnean Society*, **95**, 719-733.
- Münster-Swendsen, M. & Calabuig, I. (2000) Interaction between the solitary bee *Chelostoma florissomne* and its nest parasite *Sapyga clavicornis* - empty cells reduce the impact of parasites. *Ecological Entomology*, **25**, 63-70.
- Pasteels, J.M., Grégoire, J.-C. & Rowell-Rahier, M. (1983) The chemical ecology of defense in arthropods. *Annual Review of Entomology*, **28**, 263-289.
- Praz, C.J., Müller, A. & Dorn, S. (2008) Specialized bees fail to develop on non-host pollen: Do plants chemically protect their pollen? *Ecology*, **89**, 795-804.
- R Core Team. (2015) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rightmyer, M.G., Griswold, T. & Brady, S.G. (2013) Phylogeny and systematics of the bee genus *Osmia* (Hymenoptera: Megachilidae) with emphasis on North American *Melanosmia*: subgenera, synonymies and nesting biology revisited. *Systematic Entomology*, **38**, 561-576.
- Roulston, T.H. & Cane, J.H. (2000) Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution*, **222**, 187-209.
- Roulston, T.H. & Cane, J.H. (2002) The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). *Evolutionary Ecology*, **16**, 49-65.

- Simone-Finstrom, M.D. & Spivak, M. (2012) Increased resin collection after parasite challenge: a case of self-medication in honey bees? *Plos One*, **7**, e34601.
- Singer, M.S., Lichter-Marck, I.H., Farkas, T.E., Aaron, E., Whitney, K.D. & Mooney, K.A. (2014) Herbivore diet breadth mediates the cascading effects of carnivores in food webs. *Proceedings of the National Academy of Sciences of the USA*, **111**, 9521-9526.
- Smiley, J. (1978) Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science*, **201**, 745-747.
- Spear, D.M., Silverman, S. & Forrest, J.R.K. (2016) Data from: Asteraceae pollen provisions protect *Osmia* mason bees (Hymenoptera: Megachilidae) from brood parasitism. *American Naturalist*, *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.5064sd5009>.
- Tasei, J.-N. & Aupinel, P. (2008) Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae). *Apidologie*, **39**, 397-409.
- Therneau, T. (2014) A package for survival analysis in S. R package version 2.37-7, <http://CRAN.R-project.org/package=survival>.
- Torchio, P.F. (1972) *Sapyga pumila* Cresson a parasite of *Megachile rotundata* (F.) (Hymenoptera: Sapygidae, Megachilidae) I. Biology and descriptions of immature stages. *Melandria*, **10**, 1-22.
- Torchio, P.F. (1979) An eight-year field study involving control of *Sapyga pumila* Cresson (Hymenoptera: Sapygidae), a wasp parasite of the alfalfa leafcutter bee, *Megachile pacifica* Panzer. *Journal of the Kansas Entomological Society*, **52**, 412-419.
- Torchio, P.F. (1989) In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, **82**, 599-615.
- Wcislo, W.T. & Cane, J.H. (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology*, **41**, 257-286.
- Williams, N.M. (2003) Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). *Oecologia*, **134**, 228-237.

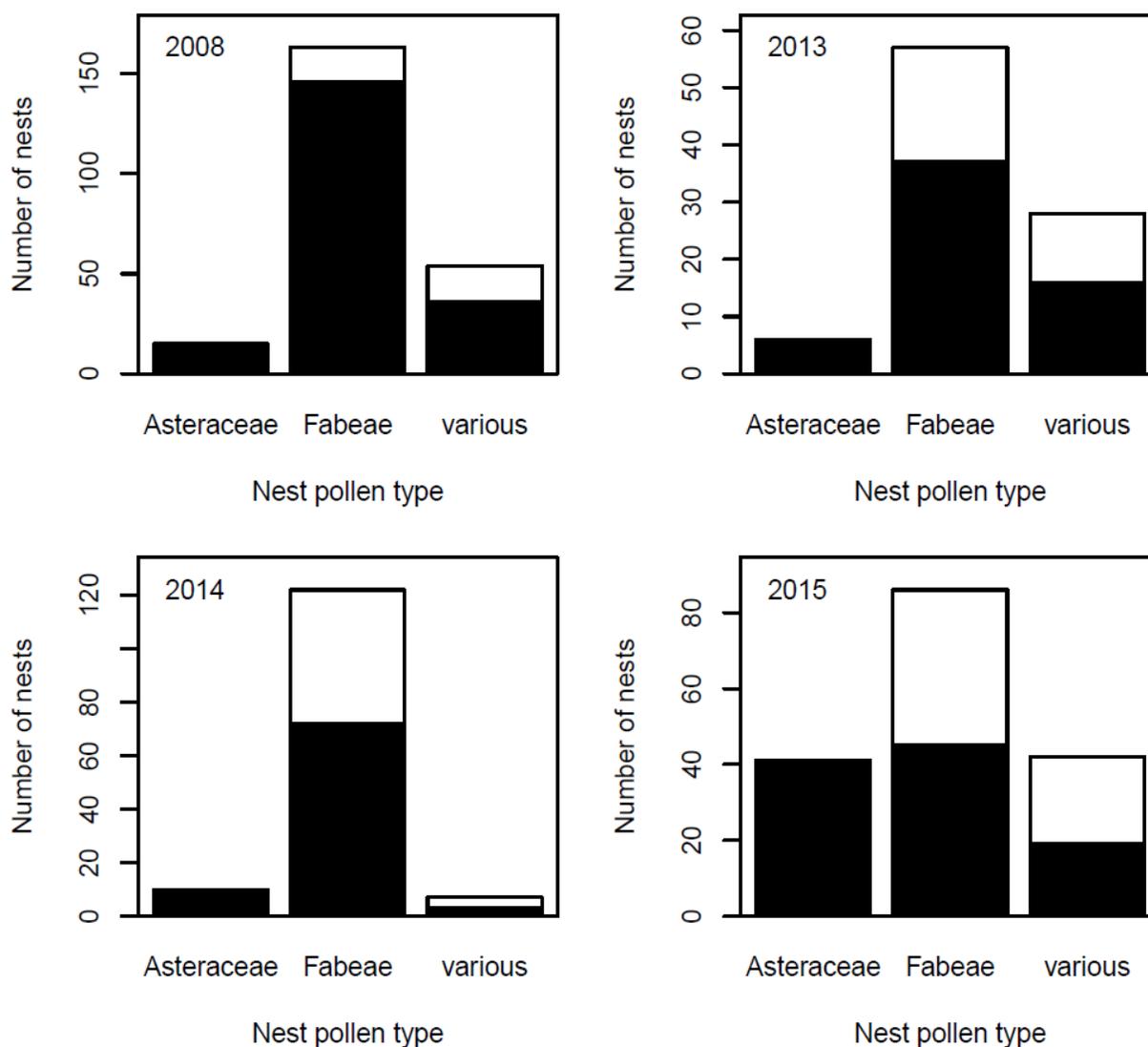


Figure 1. Incidence of parasitism by *Sapyga* in *Osmia* nests, 2008–2015. Filled portions of bars represent unparasitized nests; unfilled portions represent parasitized nests (i.e., nests in which at least one cell contained a *Sapyga* egg (2013–2015) or yielded an emerging adult *Sapyga* (2008)). Pollen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

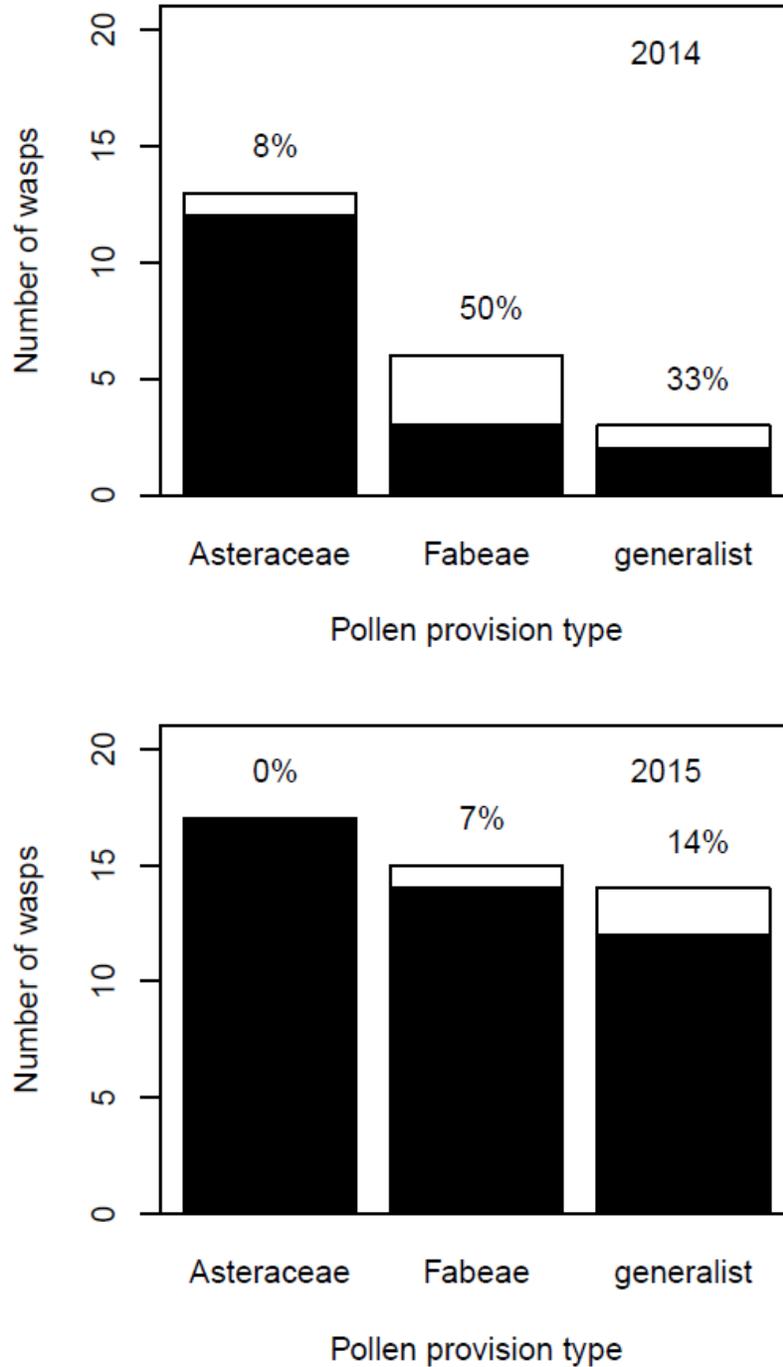


Figure 2. Numbers of sapygid wasps used in experiments in each year. Unfilled portions of bars represent wasps surviving to defecation stage; filled portions represent those not surviving to defecation. Percentages surviving to defecation are indicated above each bar.

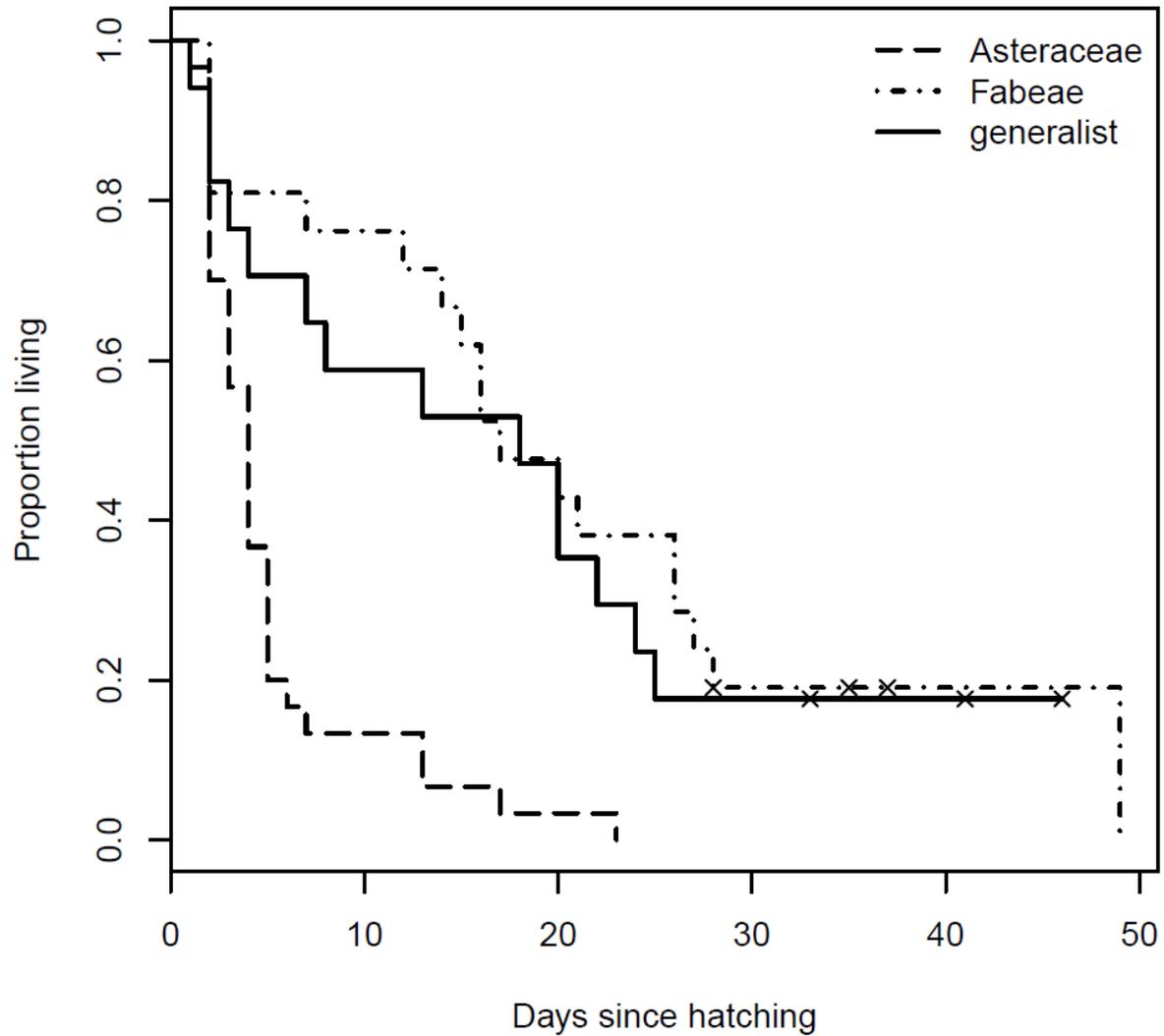


Figure 3. Kaplan-Meier survival curves for wasps raised on Asteraceae ($N = 30$), generalist ($N = 17$) or Fabae ($N = 21$) pollen provisions. Data are censored at cocoon completion for 2014 wasps, or at the end of observations for 2015 wasps (“x” on curves).

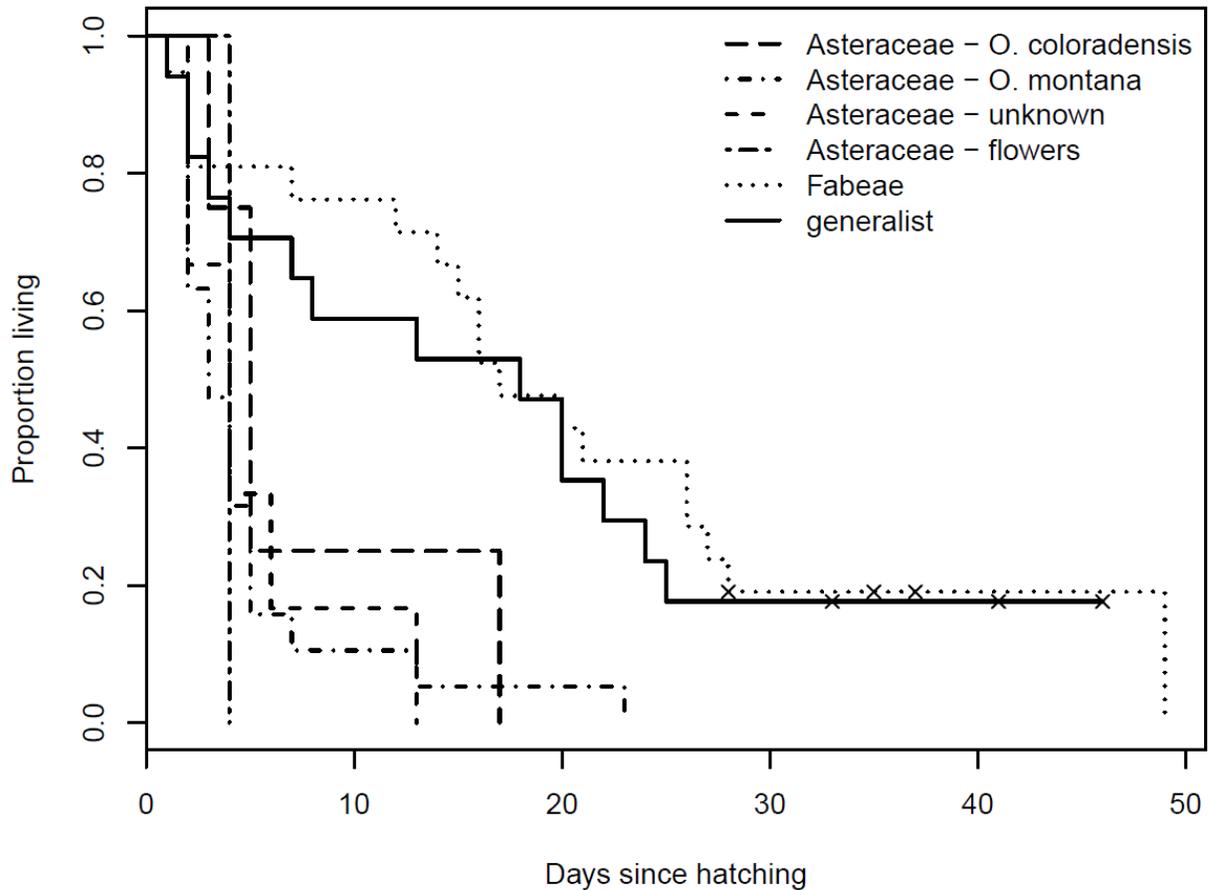


Figure A1. Kaplan-Meier survival curves for wasps raised on Asteraceae ($N = 30$), generalist ($N = 17$), or Fabeae ($N = 21$) pollen provisions. Asteraceae pollen provisions came from different sources: $N = 4$ from nests of *Osmia coloradensis*, $N = 19$ from nests of *O. montana*, $N = 6$ from nests of unknown bees, and $N = 1$ directly from flowers. Data are censored at cocoon completion for 2014 wasps, or at the end of observations for 2015 wasps (“×” on curves).