



Co-dependency between a specialist *Andrena* bee and its death camas host, *Toxicoscordion paniculatum*

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Abstract

Among associations of plants and their pollinating bees, mutually specialized pairings are rare. Typically, either pollen specialist (oligolectic) bees are joined by polylectic bees in a flowering species' pollinator guild, or specialized flowers are pollinated by one or more polylectic bees. The bee *Andrena astragali* is a narrow oligolectic, collecting pollen solely from two nearly identical species of death camas (*Toxicoscordion*, formerly *Zigadenus*). Neurotoxic alkaloids of these plants are implicated in sheep and honey bee poisoning. In this study, *T. paniculatum*, *T. venenosum* and co-flowering forbs were sampled for bees at 15 sites along a 900-km-long east–west transect across the northern Great Basin plus an altitudinal gradient in northern Utah's Bear River Range. Only *A. astragali* bees were regularly seen visiting flowering panicles of these *Toxicoscordion*. In turn, this bee was never among the 170 bee species caught at 17 species of other prevalent co-occurring wildflowers in the same five state region (38,000 plants surveyed). Our field pollination experiments show that *T. paniculatum* is primarily an outcrosser dependent on pollinator visitation for most capsule and seed set. Thus, both *A. astragali* and two sister species of *Toxicoscordion* are narrowly specialized and co-dependent on each other for reproduction, illustrating a rare case of obligate mutual specialization in bee–plant interactions.

Keywords Apiformes · Breeding biology · Monolecty · Pollination · Oligolecty · Melanthiaceae · *Zigadenus*

Introduction

Most plant–pollinator interactions include partners that are taxonomic generalists, although many also involve specialists. Rarely are both the floral host and its pollinators mutually specialized. Some brood-site mutualisms exemplify the latter, such as Neotropical figs and their fig wasps, or yuccas and their yucca moths, but these insects actively pollinate their hosts (reviewed in Proctor et al. 1996). For bees and the plants that they passively pollinate while foraging, specialization seems generally asymmetrical (Vazquez and Aizen 2004), although evidence in support of this assertion was

only mustered later by Minckley and Roulston (2006). On the one hand, diverse flowers with complex morphologies are typically pollinated by only a few generalist (polylectic) bees, such as the bumble bees (*Bombus*) that pollinate the asymmetrical flowers of *Pedicularis groenlandica* (Macior 1968). Conversely, species of oligolectic bees typically join generalists in more species-rich floral guilds (e.g. sunflowers, blueberries and willows) (reviewed in Wcislo and Cane 1996; Minckley and Roulston 2006), although the specialists are sometimes the superior pollinators (e.g. Larsson 2005).

Only a few examples represent mutually specialized bee–flower interactions, wherein a few oligolectic species are the flower's only visitors. These cases include *Macropis* bees foraging only at *Lysimachia* in the Holarctic (Vogel 1976); Brazilian *Ancyloscelis gigas* bees at *Eichhornia azurea* (Alves dos Santos and Wittmann 2000); Brazilian *Ceblurgus longipalpis* bees at *Cordia* (Milet-Pinheiro and Schlindwein 2010); several *Euryglossa* (*Euhesma*) bee species at Australian *Verticordia* (Houston et al. 1993), and in South Africa; *Rediviva* bee species at *Diascia* (Vogel and Michener 1985) or certain orchids (Pauw 2006). Half of these examples involve bees specialized to collect (Neff

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and Simpson 1981) and metabolize floral oils, although some oil-collecting bees are more taxonomically versatile (Schlindwein 1998). These narrow oligoleges are expected to be effective pollinators of their singular hosts, but evidence is sparse (Milet-Pinheiro and Schlindwein 2010).

A tantalizing additional example involves two intergrading species of death camas, *Toxicoscordion paniculatum* (Nuttall) Rydberg and *T. venenosum* (S. Watson) Rydberg (Zomlefer and Judd 2002). These are visited by a non-social bee species with the unfortunate epithet of *Andrena* (*Euan-drena*) *astragali* Viereck and Cockerell (Tepedino 2003). Pollen loads taken from female *A. astragali* in the PIRU museum collection invariably consisted of *Toxicoscordion* pollen but never included *Astragalus* pollen; that host record is only known from Cockerell's single holotype specimen (Tepedino 2003). This bee's apparent pollen specificity is consistent with it being an oligolege of *Toxicoscordion*, although it might instead merely reflect strong floral constancy for *Toxicoscordion*, the plant at which all the females had been collected. For the plant's part, its dependence on pollinators cannot be concluded, as the breeding biology of *T. paniculatum* is poorly known. Its pollen–ovule ratios suggest substantial outcrossing (Tepedino 1981), but most of the pollination trials in that study were lost to livestock trampling. Frost damaged Emms' (1993) experimental panicles, leaving only 10–15 hand-pollinated flowers to evaluate. Hence, the pollination needs of *T. paniculatum* remain unknown, and so its need for pollinators.

The three objectives of this research were (1) to experimentally characterize the breeding biology of *T. paniculatum* (and so its need for pollinators); (2) to assess the strict dependence of the bee *A. astragali* on *T. paniculatum* and *T. venenosum*, to the exclusion of other abundant co-flowering species used by other bee species in the same Intermountain wildflower communities; and (3) to document the geographical extent of their specialized relationship in the U.S. Intermountain Region using field surveys at bloom.

Materials and methods

Systematics and natural history

The taxonomic history of *Toxicoscordion* has been complex, both in tribal and familial affiliations (summarized in Zomlefer et al. 2001) as well as in generic and species circumscription. The generic assignment of North American *Toxicoscordion* has alternated with *Zigadenus* (Zomlefer and Judd 2002), but has reverted again to *Toxicoscordion* (McNeal and Zomlefer 2012). The several subtle floral characters used to distinguish *T. paniculatum* and *T. venenosum* are indistinct and overlapping, raising doubt about their specific status. For this reason, bee visitations to the two species

are combined herein. Both species are herbaceous, bulb-forming perennial geophytes. By May or June, depending on elevation, both species send up a single columnar panicle crowded with tiny, white, mostly hermaphroditic flowers with conspicuous tepal glands (Emms 1993; McNeal and Zomlefer 2012).

Breeding biology

Wild populations of *T. paniculatum* growing up Logan Canyon (Cache Co, Utah, USA) were used for experimental manual pollinations. During May and June, budded panicles were enclosed in fine mesh bags and each assigned a pollination treatment. Two manual pollination treatments—geitonogamy (transfer of self pollen) and xenogamy (outcrossing)—were applied thrice weekly to all open flowers of tagged panicles. By repeatedly hand-pollinating flowers on the same panicles over multiple days, we should have accommodated their protandrous tendencies (Emms 1993). Geitonogamous pollination involved manually rubbing recipient virgin stigmas with anthers of a flower clipped low on the same panicle. Donor flowers for xenogamy were taken from other plants in the local population. Optical visors were necessary to magnify all manipulations. Control panicles limited to autogamy remained bagged during bloom, while openly pollinated panicles were tagged but not bagged. Flowers were too small to emasculate in the field, so we cannot rule out the possibility of some geitonogamy resulting from stigmas inadvertently contacting pollen rubbed on the bagging fabric. Once seeds were nearing maturity, but before capsules had fully opened, each panicle's capsules were counted, harvested and returned to the laboratory to count their complements of plump brown seeds.

Treatments were compared for proportions of panicles producing no capsules using logistic regression. This first analysis was necessary because some treatments, especially autogamy, seldom yielded capsules. The excess of zero values (no capsules) resulted in hopelessly non-normal data that precluded an ANOVA. Convergence criteria were met for the logistic regression, however, and the proportional odds assumption accepted. The Wald test was the appropriate overall statistical test in this logistic analyses, given the sample sizes.

Reproductive responses of plants to the three manipulative treatments (autogamy, geitonogamy, xenogamy) and freely visited were then compared for all panicles that produced at least one capsule. The three measured response variables were (1) capsules per panicle; (2) total seeds per panicle; and (3) average number of seeds formed per capsule on a panicle. Square root transformation for seed counts corrected data skew. Normality of transformed data was checked by the Kolmogorov–Smirnov test (acceptable *P* values > 0.005). Homogeneity of variances was checked by Levene's test

(acceptable P values > 0.005). Because treatment was fixed but panicle (plant) was random, a mixed model ANOVA was used (Proc MIXED) (Littell et al. 1996). Following a significant overall ANOVA, treatments were compared using an *a posteriori* multiple range test (least square difference), and one *a priori* contrast was made between autogamy + geitonogamy versus outcrossing + freely visited.

Means are reported with their associated standard errors; degrees of freedom are given in subscript brackets for test statistics.

Pollinator faunas

Bees were surveyed at flowers of *Toxicoscordion* at 15 sites sampled over 16 years along a latitudinal transect 900 km long from Oregon eastward through Idaho, Nevada and Utah to Wyoming (Fig. 1), all in sagebrush-steppe and juniper woodlands. Additional montane surveys in northern Utah's Bear River Range recorded *A. astragali* visiting *Toxicoscordion* and other co-flowering species. In addition, bee guilds at wildflowers that bloomed concurrently with local *Toxicoscordion* were systematically sampled at 28 sites across the same five-state region. Representative individuals are vouchered in the PIRU collection, whose database of 1.8 million specimen label records was queried for relevant bee–host associations.

Results and discussion

Breeding biology

The probabilities of capsule formation varied with pollination treatment ($G = 17.1, P \leq 0.0007$). Of 104 panicles used, 36 set no capsules (Fig. 2). Outcrossing was fivefold more likely to yield panicles with some capsules than were either autogamy ($P \leq 0.024$) or geitonogamy ($P \leq 0.0005$)

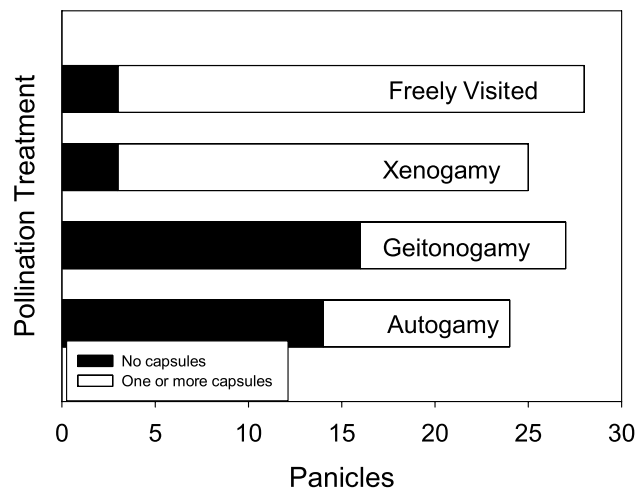


Fig. 2 Proportions of *T. paniculatum* plants whose flowering panicle yielded at least one capsule in response to pollination treatment

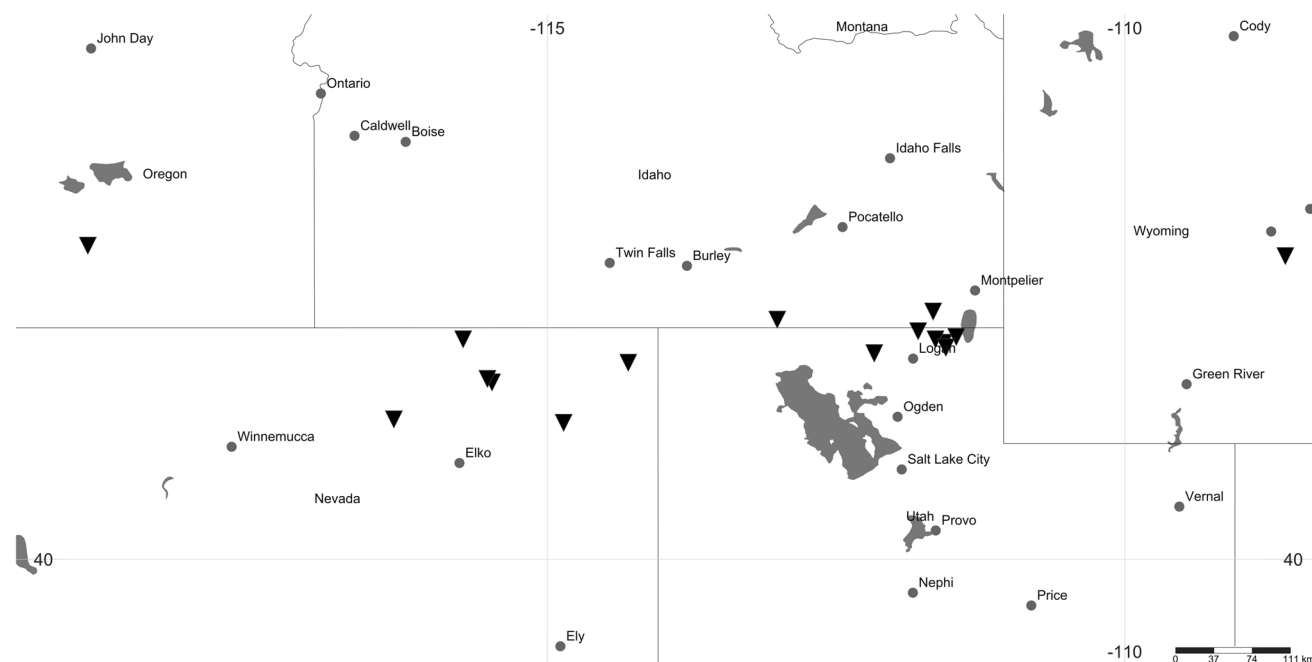


Fig. 1 Map of the northern U.S. Intermountain West showing sites where flowering populations of *T. paniculatum* or *T. venosum* were surveyed for bees (black inverted triangles)

(Table 1). Outcrossing was equivalent to open visitation in almost always generating one or more seeded capsules per panicle ($P=0.13$) (Table 1; Fig. 3a).

Seed production per each of the 68 panicles with at least one capsule also varied significantly among pollination treatment groups ($F_{[3,64]}=3.3$, $P<0.026$) (Table 1). For 105 capsules taken from untreated plants, seed content averaged 8.2 ± 0.5 seeds (range 1–27). Yields of seed of experimental plants were similar between autogamy and geitonogamy ($P>0.4$) and between outcrossed and openly visited panicles ($P>0.7$) (Table 1). The combination of xenogamy and openly visited panicles set more seeds per panicle than autogamy and geitonogamy combined ($F=9.3$, $P<0.003$) (Table 1). Among the 51 autogamy and geitonogamy panicles, 3/4 of their total seed production came from just four of their most productive plants (Fig. 3b). In contrast, the four most productive panicles that had been outcrossed or freely visited contributed 55 and 40% of total seed production to those respective treatments. Thus, proportionately

Table 1 Capsule and seed production resulting from pollination treatments applied to panicles of *T. paniculatum*

Treatment	Panicles			Sum of capsules	Sum of seeds ¹
	Number treated	Lacking capsules	Pct. lacking capsules (%) ¹		
Autogamy	24	14	58 ^A	72	367 ^a
Geitonogamy	27	16	59 ^A	115	584 ^a
Outcross	25	3	12 ^B	274	2163 ^b
Freely visited	28	3	11 ^B	371	2604 ^b

¹Treatments with different superscript letters differed significantly from one another

more outcrossed or freely visited plants contributed to sexual reproduction in their populations (Fig. 3a, b). For every seed set by autogamy or geitonogamy, 3.5 to sixfold more seeds resulted at manual outcrossed or openly visited panicles. Sexual reproduction by *T. paniculatum* mostly depends on pollinator visitation because the species is largely self-incompatible.

Pollinator fauna

With rare exception, the sole bee found visiting flowers of *Toxicoscordion* was *A. astragali*, both occasional males and many pollen-collecting females of this solitary, ground-nesting bee. Their association extended over a wide range of both latitude (Fig. 1) and elevation (1430–2330 m), from basin sagebrush-steppe to montane meadows during the months of May and June. One additional bee species, *Andrena* (*Trachandrena*) *amphibola* (Viereck), was infrequently caught at *T. paniculatum*. One relatively young (no wing wear) female was taken from death camas at each of three sites along the ID-NV border in June 2017. This bee species generally flies in midsummer (LaBerge 1973) after *T. paniculatum* bloom has past. In the PIRU collections, 85% of the 149 female specimens of *A. amphibola* lack floral host labels. However, of the 23 females with floral labels, only six were caught visiting *Toxicoscordion* (as *Zigadenus*). The remaining 17 specimens were taken at flowers of 10 genera representing eight eudicot families. In contrast, 91% of the 53 female specimens of *A. astragali* with floral host labels were taken at *Toxicoscordion*. Excepting a single bumblebee seen briefly landing on several death camas panicles before departing, no other bee but *A. astragali* was seen visiting flowers of *Toxicoscordion* in 15 populations in five states (Fig. 1), although diverse and abundant spring bee communities were active at many of these locations. In Kansas,

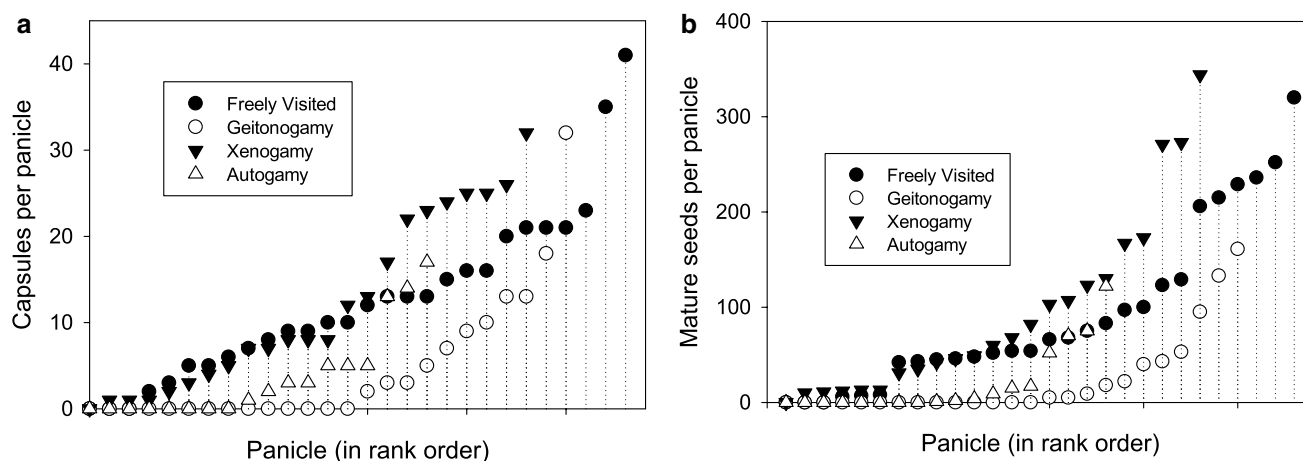


Fig. 3 Reproductive responses of panicles receiving one of four pollination treatments: **a** capsules per panicle and **b** mature seeds per panicle

flowers of another death camas (*T. nuttallii*) attracted numerous *Dialictus* sweat bees (Tepedino et al. 1989). At some but not all sites, flowers of *T. paniculatum* were also visited by the syrphid fly *Eristalis hirta* Loew, as Tepedino (1981) reported earlier. These flies were seen daubing the anthers with their proboscises; three dissected individuals had yellow pollen in their guts. Unfortunately, I neglected to consistently record their presence when surveying *Toxicoscordion* for bees.

Throughout the same 5-state region (Fig. 1), *A. astragali* was absent from systematic bee surveys at flowers of 17 species of prevalent, co-flowering floral hosts in these same habitats. The sole exception was one male *A. astragali* caught at *Lomatium dissectum* (Apiaceae). Bees visiting these dominant wildflower species were quantitatively sampled over 15 years by Cane and Love (2016). In all, 38,000 flowering plants were inspected for floral visitors, yielding > 3800 individual bees representing > 170 native bee species; none were *A. astragali*. For 28 basin sagebrush-steppe sites with flowering *Toxicoscordion*, an average of 12 other wildflower species were flowering concurrently, most commonly 1–2 species each of *Astragalus*, *Balsamorhiza*, *Delphinium*, *Eriogonum*, *Lomatium*, *Lupinus* and *Phlox*, representing six eudicot families. No species of Liliaceae *sensu lato* or Melanthiaceae were flowering at the time. In four montane plant communities of the Bear River Range in Northern Utah, *A. astragali* was regularly seen visiting flowers of *T. paniculatum* but never any of the other 17–39 blooming wildflower species, which did include several monocots (*Allium*, *Brodiaea*, *Smilacina* and *Triteleia*). Not all *Toxicoscordion* attract bees; during several hours of observing large alpine patches of blooming *T. elegans* over multiple years in the Bear River Range, no bee was ever seen visiting its flowers. These surveys document both that *A. astragali* is consistently the sole bee to regularly forage at these two sister species of *Toxicoscordion*, and that it eschews the many other co-flowering species used by diverse other wild bees in these same habitats, thus fulfilling a key criterion for claims of mutual specialization (Minckley and Roulston 2006).

In the PIRU collection database, 816 females of the 16 other species of *Euandrena* bees (the subgenus of *A. astragali*) have floral hosts labels, but only 3% (27) were caught at any other monocot flower, and none at *Toxicoscordion* or any Melanthiaceae. Several species appear to be oligoleges, but for other plant families (e.g. Asteraceae for *A. lawrenci*). Conversely, no other bee in the collection database had a floral label from any other Melanthiaceae found in North America (e.g. *Trillium*, *Veratrum*, *Xerophyllum*). Thus, there are no phylogenetic antecedents for the close association between *A. astragali* and *Toxicoscordion*, in contrast with findings of sister species of some other oligolectic genera

of bees sometimes specializing on the same or related floral host genera (e.g. Sipes and Tepedino 2005).

This study bolsters the assertion that *A. astragali* bees and the species of *Toxicoscordion* that they visit for pollen and nectar are indeed mutually reliant upon each other for reproduction. Tepedino (2003) was convinced of this bee's narrow oligolecty after finding that *Toxicoscordion* pollen composed an average of $83 \pm 11\%$ of the pollen in large loads borne by 49 female *A. astragali* specimens housed in the PIRU collection. Taken alone, that data could also merely indicate floral constancy, inasmuch as the bees were collected at *Toxicoscordion*. Floral survey data presented here show that the bee was only ever seen visiting flowers of *Toxicoscordion*, to the exclusion of other prevalent co-flowering plants, across a wide geographic region. Because all evidence indicates that *Toxicoscordion* species are the sole pollen host of *A. astragali*, the bee's reproductive dependence on death camas is apparent, although the most convincing proof of narrow oligolecty would come from larval pollen provisions taken across a series of sites, should nests ever be found.

The dependence of *T. paniculatum* on pollinators is shown by experiments with its breeding biology. Most capsules and seeds result from transfer of pollen between plants, as mediated by floral visitors. Wide-ranging field surveys show that *A. astragali* is the sole bee species visiting its flowers. Occasionally, the syrphid fly *E. hirtus* also was seen visiting death camas flowers as evidenced in earlier studies (Tepedino 1981; Emms 1993) and this study. The fly's effectiveness as a second candidate pollinator of *Toxicoscordion* needs evaluation (as is generally the case for many flower-visiting syrphid flies). Documenting single-visit pollination efficacies of *A. astragali* and this fly would be logistically daunting, but perhaps single-visit pollen deposition could be quantified despite its tiny crowded flowers. Even including the fly, it is clear that *T. paniculatum* is pollinated by at most two species of floral visitors despite its readily accessible floral rewards and the hundreds of other bee species active when and where it blooms.

Pollen and nectar rewards produced by *T. paniculatum* (and *T. venosum*) go largely uncontested, likely because they are broadly toxic to bees. Vegetative tissues of the plants contain the neurotoxic steroidal alkaloid zygacine in sufficient quantities to kill sheep (Welch et al. 2013). Zygacine targets neural sodium channels, as do the pyrethroid insecticides which are also broadly toxic to bees but tolerated by some flies (Soderlund and Knipple 2003). Spring-time kills of honey bees have been associated with death camas (Vansell and Watkins 1933). When *T. venosum* pollen was blended with sugar syrup and fed to 100 caged honey bees, they all died within 48 h (Hitchcock 1959). Inasmuch as worker honey bees will also die of starvation in that amount of time, whether the toxin killed them or dissuaded them from feeding remains an open and relevant question

for explaining the absence of all bee species but *A. astragali* at flowers of these *Toxicoscordion* species. Demonstrating apparent tolerance of dietary zygacine by adult *Eristalis* flies and adult and larval *A. astragali* bees will require quantifying the presence, if any, of zygacine in *Toxicoscordion* pollen and nectar, followed by bioassays to evaluate feeding deterrence and/or mortality resulting from biologically relevant ingested doses of this alkaloid.

The mechanism that enforces this tight mutual specialization of narrowly oligolectic *A. astragali* bees and their few *Toxicoscordion* floral hosts is clearly different from those that define the few other cases of such mutual specialization (e.g. floral oils, heterostyly).

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