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Sunflower Stem Weevil and Its Larval Parasitoids in Native Sunflowers: Is Parasitoid Abundance and Diversity Greater in the U.S. Southwest?

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ABSTRACT Classical biological control programs often target a pest’s region of origin as a likely source for new biological control agents. Here, we use this approach to search for biological control agents of the sunflower stem weevil (Cylindrocopturus adspersus LeConte), an economically important pest of commercial sunflower. We conducted surveys of weevil natural enemy diversity and abundance across a transect running from the northern Great Plains to the southwestern U.S. (the presumed area of endemism of annual sunflower species in the genus Helianthus). Accordingly, natural enemy diversity and abundance were expected to be greater in the southwestern U.S. C. adspersus and their larval parasitoids were collected from stems of four native sunflower species (Helianthus annuus, H. nottallii, H. pauciflorus, and H. petiolaris) from 147 sites across eight states. Native H. annuus constituted the majority of the sunflower populations. Mean weevil densities were significantly higher in sunflower stalks that were larger in diameter. Mean weevil densities within sites did not differ across the range of longitudes and latitudes sampled. After accounting for the effects of stalk diameter and location, weevil densities did not differ among the four sunflower species nor did they differ as a function of elevation. C. adspersus in H. annuus and H. petiolaris were attacked by seven species of parasitoids. No parasitoids were found attacking C. adspersus in H. nottallii or H. pauciflorus stalks. C. adspersus were twice as likely to be attacked by a parasitoid when feeding on H. petiolaris than H. annuus. Furthermore, the likelihood that C. adspersus would be parasitized decreased with increasing elevation and increasing stem diameters. All parasitoid species have been previously reported attacking C. adspersus larvae in cultivated sunflower. Species richness was less diverse in these collections than from previous studies of cultivated sunflower. Our findings suggest that the species of larval parasitoids attacking C. adspersus in native sunflowers have successfully made the transition to cultivated sunflower.

KEY WORDS native sunflowers, Cylindrocopturus adspersus, parasitism, native versus cultivated

A key concept in the practice of classical biological control is the notion that the area of endemism for the progenitor of a crop plant is also likely the area with the highest diversity and abundance of pest herbivores and their natural enemies (Fischorn-Walcher 1963, 1977, Kfir 1998, Hoddle et al. 2002, Kenis et al. 2005). Therefore, such areas are expected to provide the best prospects for finding effective biocontrol agents (van Driesche et al. 2008). The implicit logic behind this argument is that parasitoid–herbivore–plant associations found in native ranges have longer-established, co-evolved relationships. Such long-term, co-evolved associations are frequently composed of species-rich groups of specialized herbivores and natural enemies that are derived from generalist relationships (Schluter 1996, 2000, Stireman et al. 2006). Therefore, specialized natural enemies are expected to be more likely found in areas where plant and herbivore have co-evolved. While these ideas have been applied largely to classical biocontrol efforts involving introduced crop plants and their introduced herbivorous insect pests (van Driesche et al. 2008), the same concepts can be applied to native pests of native crop plants.

Unlike most crops grown in the United States, cultivated sunflowers (Helianthus annuus L.), along with other members of the genus Helianthus and their associate herbivores and parasitoids, are native to North America. In particular, the 13 sunflower species comprising the Section Helianthus within the genus Helianthus have southwestern U.S. distributions (Rieseberg et al. 1991, Seiler and Rieseberg 1997). In this study, we examine the diversity and abundance of parasitoids of the sunflower stem weevil, Cylindrocopturus adspersus (LeConte) (Coleoptera: Curculionidae), in a transect running from North Dakota to Arizona in western North America.

C. adspersus was first noted as a pest of sunflower by Newton (1921) who observed severely wilted plants in fields in Colorado. Damage because of feeding by the weevil continues to result in significant annual economic

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losses to cultivated sunflower crops exceeding $27 million in North Dakota, South Dakota, Minnesota, Texas, Colorado, Nebraska, and Kansas (Berglund 2007) where C. adspersus is a perennial pest (Schulz 1978, Rogers and Jones 1979, Charlet et al. 1997, Armstrong et al. 2004, Berglund 2007, Merrill et al. 2010). Approximately 20% of sunflower crop is lost because of C. adspersus larval feeding and the resultant lodging of plants whose stems have been weakened (Rogers and Jones 1979, Charlet 1987, National Sunflower Association 2006). C. adspersus is also a vector of sunflower pathogens, including Phoma black stem (Phoma macdonaldivii Boerma), which has been implicated as one of the major biotic causes of premature ripening syndrome (early dry down) of sunflower in the northern Plains (Gaudet and Schulz 1981, 1984, Charlet and Gulya 1984, Gulya and Charlet 1984). C. adspersus may also predispose plants to infection by Macrophomina phaseolina (Tassi) Goid, the pathogen associated with charcoal stem rot in sunflower in the southern Plains (Yang et al. 1983).

In addition to cultivated sunflower, C. adspersus has been collected from several native sunflower species, including H. annuus, H. pauciflorus Nuttall, H. petiolaris Nuttall, H. tuberosus L., and H. maximiliani Schrader (Charlet 1985a, Charlet et al. 1992). Several other plant species have also been noted as hosts of C. adspersus including ragweed (Ambrosia spp.), pigweed (Amaranthus spp.), Russian knapweed (Centaurea repens L.), lamb'squarter (Chenopodium album L.), golden ragwort (Senecio aureus L.), perennial sowthistle (Sonchus arvensis L.), red clover (Trifolium pratense L.), cocklebur (Xanthium strumarium L.), kochia (Kochia scoparia L.), and sugar beets (Beta vulgaris L.) (Mitchell and Pierce 1911, Pierce 1916, Goeden and Ricker 1975, 1976, Casals-Bustos 1976, Schulz 1978).

Adult C. adspersus emerge from dead, overwintered stalks of cultivated sunflower beginning in early to mid-April in the southern Plains and mid- to late June in the Northern Plains. Females deposit eggs under the epidermis at the base of young, growing sunflower stalks. Weevil larvae feed on the cortex and vascular tissue (within the first 2 mm of the epidermis) as young instars and tunnel into the pith as they mature. Mature larvae (5–6 mm long) descend to the base of the stalk or root crown at the end of the growing season and overwinter inside chambers chewed into the stalk cortex (Rogers and Jones 1979, Rogers and Serda, 1982, Charlet 1987). Overwintering larvae avoid freezing through supercooling by accumulating high levels of trehalose in their hemolymph (Rojas et al. 1994). Larvae pulate in these chambers in the spring, from which adults emerge by chewing through the stalk epidermis (Rogers and Serda 1982).

A number of species of larval parasitoids have been reported from North Dakota, South Dakota, Minnesota, Kansas, Colorado, Nebraska, and Texas to attack C. adspersus in native and cultivated sunflower. All were Hymenoptera and included three braconids (Nealioius curculionis Fitch, N. collaris Brues, Bracon sp. Braconidae), four pteromalids (Neocatalacoccus tylodermae Ashmead, Chloroecus sp., Pteromalus sp., Mesopolobus sp.), one eulophid (Quadristichus ainsliei Gahan), one eurytomid (Eurytoma tylodermatism Ashmead (Eurytomidae), and one eupelmid (Eupelmus sp.) (Rogers 1990, Rogers and Serda 1982, Charlet 1983a,b, Armstrong 1997, Charlet 1999). Generally, these parasitoids attack young C. adspersus larvae as they are feeding on the vascular and cortex tissues of the sunflower stem. In addition, North American museum records include Bhaconotus cressoni Muesebeck & Walkley (Braconidae), Eupelmus cushmani (Crawford), and E. cyanipes (Ashmead) (Euvelmidae) (Krombein et al. 1979). Surveys of cultivated sunflower have found parasitoid species diversity to be greater in the central Plains than the northern Plains (Charlet et al. 2002). Few studies have been conducted to determine the parasitoid fauna associated with the C. adspersus in host plants other than H. annuus. However, in the case of native sunflowers (Helianthus spp.) from the northern Plains, the same parasitoid species have been shown to attack weevils in cultivated and native hosts (Charlet 1983a, Charlet et al. 1992).

In this study, we surveyed native Helianthus spp. populations in a broad transect running from North Dakota to Arizona. This transect covers much of the primary areas of commercial sunflower cultivation in North America (central and northern Great Plains) as well as the putative area of endemism for the genus Helianthus (southwestern U.S.). We hypothesize that plants in southwestern U.S. Helianthus populations will harbor the greatest number of C. adspersus larvae and that parasitism rates and diversity of parasitoid species will be greatest in these populations as the southwestern U.S. is thought to be an area of origin for annual sunflowers (Helianthus L. sect. Helianthus) (Heiser et al. 1969, Rogers et al. 1982, Rieseberg et al. 1991). To examine these predictions, we measured the incidence of C. adspersus larvae and their rates of parasitism by various species of larval parasitoids and correlated these measures with elevation, location (latitude and longitude), stem diameter, and sunflower species. We compare our findings of the prevalence of C. adspersus parasitoids in native Helianthus populations with previously published surveys of C. adspersus parasitoids on cultivated sunflower populations. We predict that native Helianthus populations, particularly those in the southwestern U.S., will harbor a greater diversity of parasitoids than cultivated H. annuus populations.

Materials and Methods
The survey was conducted in early autumn of 2003 and 2005 to collect mature C. adspersus larvae overwintering in stalks of four Helianthus species: the annual species H. annuus and H. petiolaris, and the perennial species H. nutallii Torrey and Gray and H. pauciflorus. Populations of H. annuus were selected as wild populations based on wild species traits with no obvious out crossed plants (see Seiler and Rieseberg 1997). Locations near to cultivated fields were avoided to reduce the likelihood of cross pollination with cultivated H. annuus. Wild H. annuus is widely distributed with considerable variation in all traits, but no plants
in the wild populations examined were classified as wild outcrosses.

Survey sites were selected at random irrespective of population size such that they were at least 30 km apart. In 2003, 1239 sunflower stalks containing 4,252 C. adspersus larvae from 72 locations were collected in North and South Dakota, Nebraska, Kansas, Colorado, and Wyoming between 22 and 26 September. In 2005, 1,360 sunflower stalks containing 5,563 C. adspersus larvae were collected from 75 sites in southern Colorado, New Mexico, and Arizona between 2 and 9 October (Fig. 1). By these dates, plants had largely senesced and weevil larvae had moved to the lower portion of the stalks near the root crown. Across both years, 147 sites were visited yielding 134 collections of H. annuus, 21 collections of H. petiolaris, one collection of H. nuttallii, and one collection of H. pauciflorus. Eight sites contained both H. annuus and H. petiolaris and one site contained H. annuus, H. petiolaris, and H. pauciflorus. From each site, 7 to 30 stalks (including the root crown) were collected and placed in paper bags, taped together, and labeled with the site identification number. Stalk samples from sites containing more than one sunflower species were placed in separate bags. The stalks were stored in a cold room at 5°C for a period of ≈2 mo to allow weevil larvae to complete diapause. After this 2-mo period, the stalks were split open to recover the overwintering larvae inside; the numbers of C. adspersus larvae per stalk were counted. Stalk diameter was measured at the plant base (≈1–2 cm above the soil level). The larvae were then placed in small, multi-chambered trays with hard plastic covers (8 × 12.5 cm with 216 individual chambers) and held in a rearing room at 24 ± 2°C, 50–60% RH, and a photoperiod of 15 h: 9 h (L:D) for emergence of adult weevils or parasitoids (Charlet 1983b). Larvae were held in these chambers until eclosion of adult weevils, emergence of parasitoids, or their death. Dead larvae were not dissected as they had often decayed preventing examination for the presence of parasitoids. Percentage parasitism was determined from the number of parasitoids recovered relative to total sunflower stem weevil larvae reared, excluding those that died. Identifications were verified based on specimens in the second author’s (L.D.C.) collection previously determined by specialists at the U.S. Department of Agriculture, ARS Systematic Entomology Laboratory (Beltsville, MD) or Texas A&M University. Voucher specimens were placed in the author’s sunflower insect collection (USDA-ARS Northern Crop Science Laboratory, Fargo, ND) and in the North Dakota State Insect Reference Collection, Department of Entomology, North Dakota State University, Fargo, ND.

The mean number of weevil larvae per stalk was analyzed as a function of stem diameter, sunflower species, collection year, location (latitude, longitude), and elevation with an analysis of covariance (ANCOVA) (PROC GLM, SAS 2008). The mean number of weevil larvae were log-transformed to achieve normally distributed residuals. No differences were seen across the two collection years (t = -1.44; P = 0.1514); therefore, data were pooled across the two collection years. The likelihood that a weevil would be attacked by a parasitoid (number of weevils parasitized out of the total number of larvae reared) was analyzed with a
logistic regression as a function of stem diameter, sunflower species, location, and elevation (PROC LOGISTIC, SAS 2008). For both analyses, quadratic terms for longitude and latitude were included to account for the possibility that weevil densities or parasitism do not vary linearly. Weevil larvae in *H. nuttallii* and *H. pauciflorus* were not found to be parasitized and were therefore excluded from these analyses.

### Results

The mean number of *C. adspersus* larvae was greater in sunflowers with larger stalk diameters (which are indicative of larger overall plant size) (Table 1; Fig. 2). Across the survey sites, the mean *C. adspersus* larval densities did not differ across the latitudes (Table 1). Mean stem weevil numbers were greatest at intermediate longitudes (Table 1; i.e., between 104 and 106°W). The mean number of *C. adspersus* per plant did not differ among the four sunflower species. Furthermore, mean weevil densities in sunflowers were not related to elevation of the collection sites (Table 1).

A total of 75 parasitoids emerged from the 2,385 stem weevil larvae that successfully overwintered from the stalks collected in 2003, but only 10 emerged from 3,001 larvae that successfully overwintered in 2005 (Table 2). No parasitoids were reared from weevil larvae collected from *H. nuttallii* or *H. pauciflorus* stalks. In 2003, parasitoid individuals identified included 28 *Quadrastichus antisielii* (Eulophidae), 14 *Neocatolaccus tylodermiae* and one *Chlorocytus sp.* (Pteromalidae), and 13 *Nealiolus curculionis*, and 1 *Nealiolus collaris* (Braconidae); in addition, 18 parasitoids did not complete development and their identity could not be determined. In 2005, the parasitoids recovered included two *N. tylodermiae*, one *N. curculionis*, one *Eurytoma tylodermatitis* Ashmead (Eurytomidae), one *Chlorocytus*, and three undetermined species. Rates of parasitism were low overall with the highest mean percent parasitism (8.3%) occurring among the collections from North Dakota. No parasitoids were recovered from stem weevil larvae recovered in stalks at the 20 collection sites for *H. annuus* and *H. petiolaris* in Arizona. All these species have previously been reported attacking sunflower stem weevil larvae in cultivated sunflower.

Weevil larvae feeding on *H. petiolaris* were 2.1 times as likely to be parasitized than larvae feeding on *H. annuus* (Table 3; Wald $\chi^2 = 4.70, P = 0.030$). Even after accounting for the effect of sunflower species on parasitism rate, the likelihood of parasitism decreased with increasing sunflower stem diameter. For each decrease in stem diameter of 1 cm, the likelihood of a stem weevil larva being parasitized also decreased with increasing elevation. For every kilometer decrease in elevation, the likelihood of parasitism decreased by 6.75 times (Table 3; Wald $\chi^2 = 9.37, P = 0.002$). Finally, the risk of parasitism was

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**Table 1.** Multiple regression parameter estimates, standard errors, $t$-values, and associated $P$ values for the ANCOVA model explaining the log-transformed mean no. of sunflower stem weevil larvae as a function of sunflower species, mean stem diam (centimeters), latitude, longitude, and elevation (1,000 m).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>$t$-value</th>
<th>$Pr &gt; t$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-496.595</td>
<td>140.622</td>
<td>-3.53</td>
<td>0.001</td>
</tr>
<tr>
<td>Sunflower: <em>H. annuus</em></td>
<td>0.511</td>
<td>0.400</td>
<td>1.28</td>
<td>0.204</td>
</tr>
<tr>
<td>Sunflower: <em>H. nuttallii</em></td>
<td>-0.634</td>
<td>1.602</td>
<td>-0.39</td>
<td>0.541</td>
</tr>
<tr>
<td>Sunflower: <em>H. pauciflorus</em></td>
<td>-0.525</td>
<td>1.622</td>
<td>-0.32</td>
<td>0.746</td>
</tr>
<tr>
<td>Sunflower: <em>H. petiolaris</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mean stem diam</td>
<td>2.453</td>
<td>0.545</td>
<td>4.50</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Latitude</td>
<td>0.150</td>
<td>0.501</td>
<td>0.22</td>
<td>0.822</td>
</tr>
<tr>
<td>Latitude*latitude</td>
<td>-0.001</td>
<td>0.010</td>
<td>-1.3</td>
<td>0.898</td>
</tr>
<tr>
<td>Longitude</td>
<td>-9.316</td>
<td>2.626</td>
<td>-3.54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Longitude*latitude</td>
<td>-0.044</td>
<td>0.012</td>
<td>-3.59</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Elevation (1000 m)</td>
<td>0.405</td>
<td>0.445</td>
<td>0.91</td>
<td>0.364</td>
</tr>
</tbody>
</table>

The overall model explained 39% of the variation in mean no. of weevil larvae ($F_{9,147} = 10.49; P < 0.0001$).

![Fig. 2. Mean number of *C. adspersus* larvae collected per sunflower stalks within a site as a function of mean stem diameter.](image-url)
similar across the latitudinal and longitudinal range of this study.

Discussion

Contrary to our predictions, southwestern U.S. populations of *Helianthus* spp. did not harbor more *C. adspersus* larvae nor did these weevil populations suffer higher parasitoid attack rates or attacks by a greater diversity of parasitoid species than populations in the central or northern Great Plains. Indeed, mean weevil densities in Arizona and New Mexico (southwestern U.S.) field sites were lower than at sites in Nebraska, Colorado, or Kansas (central Plains) and were similar to sites in North Dakota and South Dakota (northern Plains). Furthermore, parasitism rates were extremely low in southwestern U.S. field sites compared with elsewhere in the central and northern Plains. One possibility is that wild *H. annuus*, along with *C. adspersus* and its larval parasitoids, has had sufficient time to spread from the U.S. Southwest throughout the Great Plains such that differences in distribution across the entire region are trivial. Indeed, our findings suggest that latitudinal differences in weevil abundance as well as parasitism rates and diversity are minor at best after variables such as host plant species and stem diameter have been accounted for. *H. annuus* is thought to have been restricted to the southwestern U.S. before the arrival of humans who domesticated and spread sunflower to the central U.S. (Seiler and Jan 2010). While systematic data strongly suggest a southwestern U.S. origin of annual sunflowers including *H. annuus* (Heiser et al. 1969, Rieseberg et al. 1991), *H. annuus* is now widely distributed throughout the U.S., albeit it is more common in the western two-thirds of the country (Rogers et al. 1982). However, there is little agreement about how long wild *H. annuus* has occupied its current geographic range (Asch 1993). Predomestication events may have resulted in a wide distribution for wild *H. annuus* throughout the Midwest before the arrival of humans. Unfortunately, archeological records tell us little about the prehuman geographical distribution of wild *H. annuus* (Asch 1993).

Also contrary to our predictions, we did not find a higher diversity of parasitoids attacking *C. adspersus* on wild *H. annuus* populations compared with previously reported parasitoid diversity of *C. adspersus* on cultivated *H. annuus*. In a previous study of parasitism of *C. adspersus* on cultivated *H. annuus*, higher parasitoid diversity was found in fields in the central Plains (eight species) than in fields in the northern Plains (four species) (Table 2 in Charlet et al. 2002). Similarly, we found four parasitoid species on *C. adspersus* on wild *H. annuus* in populations in the northern Plains and seven parasitoid species in populations throughout the central Plains (Table 2 of this paper), none of which were new records. Unexpectedly, we recovered only two species from populations in the southwestern U.S. likely a consequence of the extremely low parasitism rates in these populations. Our data did show that parasitism rates were lower at

Table 2. Occurrence of *C. adspersus* larvae and its larval parasitoids in sunflower stalks of different sunflower species collected in eight states in the western United States in 2003 and 2005

<table>
<thead>
<tr>
<th>Year</th>
<th>State</th>
<th><em>Helianthus</em> species</th>
<th>N</th>
<th>No. larvae/plant</th>
<th>Mean</th>
<th>Range</th>
<th>N reared</th>
<th>% Larval incidence</th>
<th>Overall</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>ND</td>
<td><em>H. annuus</em></td>
<td>9</td>
<td>3.7 ± 0.5</td>
<td>62.9</td>
<td>20.0–100</td>
<td>290</td>
<td>8.3 ± 3.9</td>
<td>0–33.3</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td><em>H. annuus</em></td>
<td>12</td>
<td>2.7 ± 0.5</td>
<td>46.4</td>
<td>4.2–100</td>
<td>354</td>
<td>3.9 ± 2.4</td>
<td>0–25.9</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>NE</td>
<td><em>H. annuus</em></td>
<td>10</td>
<td>5.3 ± 1.0</td>
<td>64.4</td>
<td>23.1–100</td>
<td>661</td>
<td>0.4 ± 0.2</td>
<td>0–3.0</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>H. petiolaris</td>
<td>9</td>
<td>1.1 ± 0.2</td>
<td>46.0</td>
<td>17.6–85.7</td>
<td>114</td>
<td>6.4 ± 3.5</td>
<td>0–28.6</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>H. pauciflorus</td>
<td>1</td>
<td>0.1 ± 0.1</td>
<td>13.3</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td></td>
<td>H. nuttallii</td>
<td>1</td>
<td>0.2 ± 0.1</td>
<td>13.3</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td></td>
<td>KS</td>
<td><em>H. annuus</em></td>
<td>9</td>
<td>7.8 ± 1.2</td>
<td>66.5</td>
<td>10.0–100</td>
<td>510</td>
<td>5.6 ± 2.0</td>
<td>0–28.6</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>CO</td>
<td><em>H. annuus</em></td>
<td>11</td>
<td>5.3 ± 1.1</td>
<td>55.0</td>
<td>9.1–100</td>
<td>362</td>
<td>0.4 ± 0.3</td>
<td>0–2.4</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>H. petiolaris</td>
<td>3</td>
<td>2.1 ± 0.3</td>
<td>74.0</td>
<td>45.0–90.0</td>
<td>79</td>
<td>3.0 ± 0.0</td>
<td>0–9.1</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WY</td>
<td><em>H. annuus</em></td>
<td>7</td>
<td>1.3 ± 0.3</td>
<td>39.2</td>
<td>16.7–80.0</td>
<td>52</td>
<td>1.1 ± 1.1</td>
<td>0–7.9</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>H. petiolaris</td>
<td>1</td>
<td>0.1 ± 0.1</td>
<td>14.3</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>2005</td>
<td>CO</td>
<td><em>H. annuus</em></td>
<td>25</td>
<td>7.2 ± 0.6</td>
<td>72.3</td>
<td>7–100</td>
<td>1822</td>
<td>0.3 ± 0.1</td>
<td>0–1.4</td>
<td>2,3,6,7</td>
</tr>
<tr>
<td></td>
<td>H. petiolaris</td>
<td>1</td>
<td>2.5 ± 0.6</td>
<td>88.2</td>
<td>26</td>
<td>26</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NM</td>
<td><em>H. annuus</em></td>
<td>27</td>
<td>3.3 ± 0.4</td>
<td>57.3</td>
<td>11.1–100</td>
<td>786</td>
<td>0.04 ± 0.04</td>
<td>0–4.0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>H. petiolaris</td>
<td>5</td>
<td>2.3 ± 0.6</td>
<td>49.2</td>
<td>21.7–75.0</td>
<td>124</td>
<td>0.2 ± 0.2</td>
<td>0–3.2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AZ</td>
<td><em>H. annuus</em></td>
<td>18</td>
<td>2.4 ± 0.3</td>
<td>49.3</td>
<td>9–133</td>
<td>243</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>H. petiolaris</td>
<td>2</td>
<td>0.01 ± 0.01</td>
<td>2.4</td>
<td>0–4.8</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
</tbody>
</table>


Table 3. Odds ratio estimates (with 95% CI), Wald χ² values, and associated P values for the logistic regression model explaining the likelihood of parasitism of sunflower stem weevil larvae as a function of sunflower species, collection year, mean stem diam (centimeters), latitude, longitude, and elevation (1,000 m)

<table>
<thead>
<tr>
<th>Effect</th>
<th>Odds ratio (95% CI)</th>
<th>Wald χ²</th>
<th>Pr &gt; χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. petiolaris vs. H. annuus</td>
<td>2.096 (1.073–4.092)</td>
<td>4.696</td>
<td>0.030</td>
</tr>
<tr>
<td>mean stem diam (cm)</td>
<td>0.375 (0.148–0.951)</td>
<td>4.266</td>
<td>0.039</td>
</tr>
<tr>
<td>elevation (1,000 m)</td>
<td>0.148 (0.004–1.503)</td>
<td>9.372</td>
<td>0.002</td>
</tr>
</tbody>
</table>

Odds ratios were not calculable for the polynomial variables longitude and latitude. Neither *H. nuttallii* nor *H. pauciflorum* harbored *C. adspersus* that were parasitized and were therefore excluded from this analysis.
higher altitudes, which may partially account for low rates of parasitism in Arizona and New Mexico as many of the collection sites at the highest elevations in this study occurred in these two states. Additional collections should be made in the southwest to confirm these conclusions.

Studies of other sunflower pests have shown that parasitoid diversity and parasitism rates are greater in native *Helianthus annuus* populations compared with cultivated populations, opposite of the pattern seen in *C. adspersus* (this study, Charlet et al. 2002). In a study of the sunflower moth, *Homoeosoma electellum* (Hulst), Charlet (1983a) and Charlet et al. (1992) reported higher numbers of *C. adspersus* larvae in *H. annuus* stems than the other sunflower species studied in North Dakota. Stems of *H. annuus* are more robust and larger in diameter than the other sunflower species, accounting for some of the difference in weevil density. Indeed, after accounting for stem diameter, sunflower species identity was not correlated with weevil numbers. Increased stem diameters associated with domestication in sunflowers appears to have increased feeding damage by *C. adspersus* in at least two ways. First, as explained above, stem diameter is positively correlated with the number of weevils feeding on a given plant. Larger plants with larger stems are able to support more feeding weevils. Second, weevils feeding within plants with larger diameter stems are significantly less likely to be parasitized. Weevils feeding within thicker stems may be more likely to escape detection by probing parasitic wasps. We were unable to directly examine this because at the time of our sampling, larvae had finished feeding and had moved to the base of the stalk in preparation for overwintering.

Interestingly, *C. adspersus* were twice as likely to be parasitized in *H. petiolaris* as compared with *H. annuus*. This was true even after accounting for the effects of location and stem diameter, variables that we have shown to be correlated with weevil density. Whether these two sunflower species differ in their attractiveness to parasitoids (e.g., Turlings and Wingfield 2004) or their negative effects on parasitoid fitness (e.g., Ode 2006) are unexplored possibilities. Sesquiterpene lactones and diterpene acids are common in most wild populations of sunflowers and associated with reduced fitness of the sunflower moth, *Homoeosoma electellum* (Hulst) (Rissler et al. 1986, Rogers et al. 1987).

We surveyed sunflower populations in the southwestern U.S., speculating that these might reveal additional species of parasitoids, because a more diverse
natural enemy complex is thought to occur in the host’s region of origin (Pschorn-Walcher 1977). Because this study produced no new records for larval parasitoids, it appears that the species of larval parasitoids attacking C. adspersus in native sunflowers have successfully made the transition to the cultivated crop to parasitize this pest species. Little is known about the abundance of C. adspersus on other 51 wild species of Helianthus, although one study suggests that weevil abundance is lower several perennial species than on wild or cultivated H. annuus (Rogers and Seiler 1985). However, additional work is needed to document whether the sunflower stem weevil is present in other Helianthus species and whether the C. adspersus natural enemy complex is similar to what has been identified to date in cultivated sunflower.

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