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Seed predation in wild populations of Chamisso arnica (*Arnica chamissonis* Less: Asteraceae) and new host records for *Campiglossa snowi* (Hering) (Diptera: Tephritidae)

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SEED PREDATION IN WILD POPULATIONS OF CHAMISSO ARNICA (*ARNICA CHAMISSONIS* LESS: ASTERACEAE) AND NEW HOST RECORDS FOR *CAMPIGLOSSA SNOWI* (HERING) (DIPTERA: TEPHRITIDAE)

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ABSTRACT.—New host records are reported for *Campiglossa snowi* (Hering), *Tephritis leavittensis* Blanc, and *Trupanea nigricornis* (Coquillett) on *Arnica chamissonis* Less. and *C. snowi* on *Arnica mollis* Hook. *Campiglossa snowi* was the only fruit fly reared from *A. chamissonis* from 3 different populations from the Kenai Peninsula, Alaska, over 5 sample years. A total of 1114 specimens of *C. snowi* were reared from the flower heads of 337 plants averaging 5 flower heads per plant. Seed damage from fly larvae ranged from 0% to 54.8% per capitulum, with an overall average of 18.3% across all years and between 3 sites on the Kenai Peninsula. Infestation rates for individual capitula and entire plants averaged 56.4% and 79.0%, respectively, across all years and sites. Fly abundance was not consistent from year to year, but peaked during 2010, with substantially lower values in years preceding and following the peak. *Campiglossa snowi* individuals reared from flower heads at additional sites and across multiple states expand the species' known distribution range.

RESUMEN.—Reportamos nuevos registros de huéspedes de la flor *Arnica chamissonis* Less: *Campiglossa snowi* (Hering), *Tephritis leavittensis* Blanc y *Trupanea nigricornis* (Coquillett), y *C. snowi* de la flor *Arnica mollis* Hook. *Campiglossa snowi* fue la única mosca de que se desarrolló en *A. chamissonis* en 3 poblaciones diferentes de la Península de Kenai, Alaska, durante 5 años de muestreo. Durante este tiempo, un total de 1,114 ejemplares de *C. snowi* crecieron en la cabeza de las flores de 337 plantas con un promedio de 5 cabezas por planta. El daño causado en las semillas debido a las larvas de mosca osciló entre 0%–54.8% por capítulo, con un promedio total de 18.3% a lo largo de todos los años de muestreo y entre 3 sitios en la península de Kenai. Las tasas de infestación de capítulos individuales y de plantas enteras mostraron un promedio de entre 56.4% y 79.0% a lo largo de todos los años y sitios respectivamente. La abundancia de moscas no fue consistente de un año a otro, pero alcanzó su máximo durante el 2010 con valores sustancialmente más bajos en los años anteriores y posteriores. *Campiglossa snowi* que se desarrolló en la cabeza de las flores en sitios adicionales y a lo largo de múltiples estados muestra una expansión de su rango de distribución conocido.

Plant host relationships of fruit flies (Diptera: Tephritidae) have worldwide research interest primarily due to economic impacts of tephritid flies on major fruit and vegetable crops (Badii et al. 2015, Walton et al. 2016). Nonfrugivorous fruit flies are also routinely studied for biological control opportunities against invasive weeds (Pitcairn et al. 2008, Skuhrovec et al. 2008, Story et al. 2008, Birdsall and Markin 2010).

Most seed-feeding fruit flies parasitize plants in the family Asteraceae (Foote et al. 1993) where flowers are arranged in a compact flower head (capitulum) and fly larvae are able to move throughout the flower head to feed on multiple seeds and flower parts (Headrick and Goeden 1998). Plants that have commercial value in the harvesting of seed or flower heads can be negatively impacted by seed predators.

This study investigates seed predation by tephritid fruit flies in wild populations of chamisso arnica (*Arnica chamissonis* Less., Asteraceae). There are 2 major potential uses of *A. chamissonis* for which seed predation may pose a concern: as a seed crop for the reclamation industry or as a pharmaceutical crop. Because of the increased interest in seed harvest from wild populations of native plants (Lippitt et al. 1994, Vander Mijnsbrugge et al. 2010, Broadhurst et al. 2015) and commercial cultivation of native plants for the reclamation industry (Shaw et al. 2005, 2012, Mock et al. 2016), the impact of fruit flies that parasitize seeds, thus affecting seed production, poses potential risks. *Arnica chamissonis* was included in the inventory of species deposited at the Royal Botanic Gardens, Kew, Millennium Seed Bank under the Bureau of Land Management's Seeds of Success program

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(De Bolt and Spurrier 2004) to "collect, conserve, and develop native plant material for stabilizing, rehabilitating, and restoring lands in the United States" (BLM 2016). Part of what makes *A. chamissonis* an attractive restoration species is its ability to colonize disturbed roadsides where its showy yellow flowers contribute to an aesthetically pleasing roadside landscape. Use of *A. chamissonis* as a reclamation species is still limited, however, primarily because it grows in areas where reclamation needs are as yet minimal.

Arnica also has potential as a pharmaceutical crop. Several *Arnica* species, including *A. chamissonis*, have been identified for pharmaceutical research where flavonoids and other compounds are harvested from the flower heads (Cassells et al. 1999, Roki et al. 2001, Saeed 2014). Extracts from these plants have recently been identified as having potential value in treating Alzheimer's disease (Russo et al. 2013), and the seeds possess a wide array of antioxidant compounds (Gawlik-Dziki et al. 2009). In order to reduce harvesting pressures on wild plants, researchers have recommended growing *Arnica* and other pharmaceutical plants under cultivation (Schippmann et al. 2002, Sugier et al. 2013). Knowledge of plant pests that can potentially reduce pharmaceutical yields could be important, especially when plants are grown as a monoculture.

In addition to the value of studying seed predation in *A. chamissonis* for reasons of commercial application, it is valuable to document the occurrence and extent of seed predation by a tephritid fruit fly on a plant with little host association information. Much of the information on nonfrugivorous tephritid host associations is no more than the association record, with information seldom provided on the extent of seed damage (Foote et al. 1993).

Arnica chamissonis is an attractive plant with yellow petals in the family Asteraceae found throughout most of western North America (Wolf 2006). It ranges from Alaska south to California and as far east as Quebec, Canada, though records of its eastern range in the United States terminate in Montana and south through Wyoming, Colorado, and New Mexico, with a recorded presence in Oklahoma (USDA–NRCS 2015) (Fig. 1). We agree with and follow the taxonomic treatment of *A. chamissonis* by Wolf (2006) in *Flora of North America* and Wolf and Barkley (2012) in *The Jepson Manual.* In their treatments, all varieties or subspecies are synonymized under the nominate *A. chamissonis* sensu lato. The degree of variation, primarily of leaf and stem pubescence, intergrades between geographical regions, making it difficult to segregate published varieties with confidence. Even determinations between recognized species can be difficult, especially when smaller specimens lack the distinguishing number of leaves per stem used in modern taxonomic keys. It is important to recognize, however, that different genotypes likely exist across the broad distribution of *A. chamissonis*, particularly if the species is used for restoration and site-adapted genotypes are desired.

While visiting Alaska during summer 2013, the authors discovered a tephritid fruit fly while sweep-netting *A. chamissonis* on the Kenai Peninsula where populations of plants are regularly encountered growing roadside. After an initial interest in recording the host association, we hypothesized that the presence of seed-predating tephritid fruit flies would have a negative impact on seed yield in *A. chamissonis* populations. To test this assumption, we sampled flower heads of *A. chamissonis* across several sites and years on the Kenai Peninsula, Alaska. We also report additional host associations of tephritid fruit flies on *Arnica* spp. from elsewhere in the western United States.

METHODS

Flower heads of *A. chamissonis* were collected in 2007, 2009, 2010, 2011, and 2013 from 3 sites on the Kenai Peninsula, Alaska. These sites were chosen during the first reconnaissance year upon encountering an adequate plant population size within the time constraints of travel. The 3 selected study sites were roadside populations in the vicinity of Seward, Alaska, and were between 200 m^2 and 500 m^2 in population area, but with estimated population sizes of >1000 plants. Site locations were Seward Tracks (60.12611, −149.43485, 21 m elevation), Salmon River (60.18186, −149.3903, 58 m elevation), and Nash Road (60.13264, −149.37935, 17 m elevation). Flower heads were collected on the following dates: 17 August 2007, 24 July 2009, 23 July 2010, 22 July 2011, and 25 July 2013. A minimum of 20 plants were randomly selected from each plant population using a

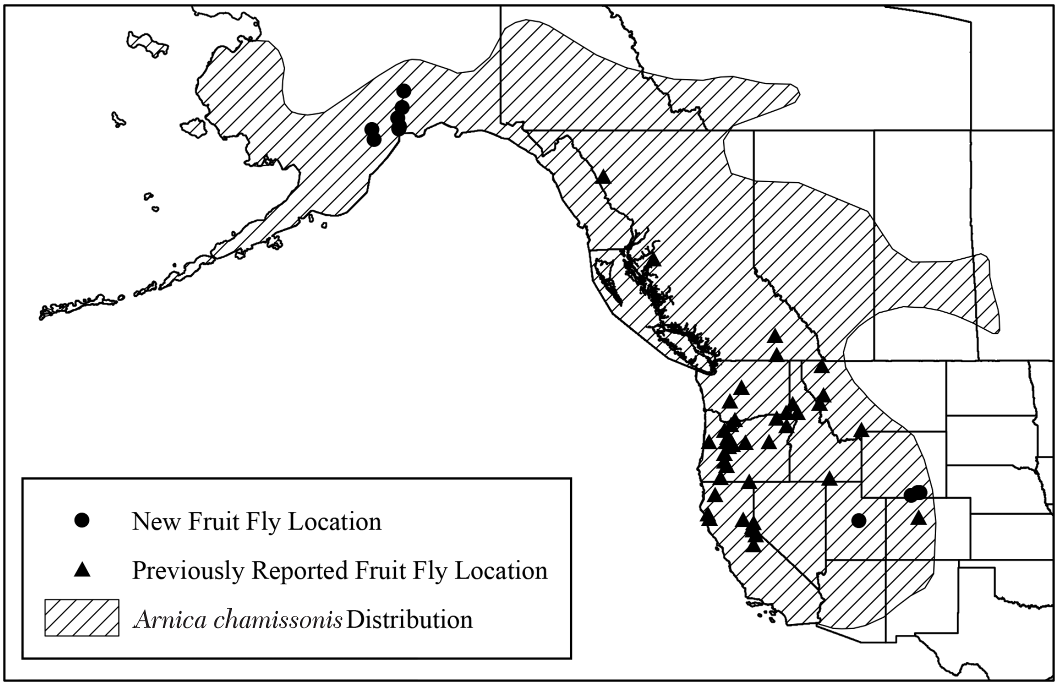

Fig. 1. Distribution of *Campiglossa snowi* and its host plant *Arnica chamissonis*. The distribution of *A. chamissonis* in North America was determined by georeferenced specimens from online herbarium databases (CMN [2014], ABMI [2015], SEINet [2009–2015], PNWH [2015]). There were also a few isolated and unconfirmed occurrences of the species in western Canada, which were not included in this figure. New *C. snowi* locations were documented by our own field research; previously known locations were documented by Richard H. Foote (Foote and Blanc 1963, Foote et al. 1993).

nearest-neighbor-to-transect-point method, with the transect(s) bisecting the population and the 20 transect points evenly distributed. All flower heads were collected at mid to late anthesis. The presence of fly pupa was confirmed by opening capitula to reveal black puparia. For the occasional flies that emerged prior to flower head collection, puparia still remained in the flower heads and was used for tallying. All flower heads from each sampled plant were sealed in a plastic bag and stored in a cooler for transport to the lab for rearing. Flower heads were then placed in plastic 4-ounce (120-mL) portion cups with perforated lids for rearing with ambient air temperatures ranging between a nighttime low of 65 °F (18.3 °C) and a daytime high of 80 °F (26.7 °C). Flower heads were left in their rearing cups for 2 months. Emerged flies were then identified and tallied.

The percent seed damage was estimated for each seed head by examining the seeds under a dissecting microscope to determine damaged versus undamaged seeds. Each flower head was opened and each seed examined. Seeds that showed larval feeding that penetrated the seed coat were counted as damaged.

Additional collections of *A. chamissonis* flower heads were made within the states of Alaska, Oregon, Wyoming, and Utah in 2013 and 2014 and reared in plastic portion cups (Table 1, Fig. 1). These additional collections were made from several road trips to locations identified from herbarium specimens as locations for *A. chamissonis*. This effort was designed to get a better picture of the distribution of tephritid host associations in areas with few association records where *A. chamissonis* occurs. These additional locations were not "study sites," as are the 3 sites from the Kenai Peninsula, but instead were sites where flower heads were collected during only a single visit. The additional survey sites were not part of the analysis of seed predation over time, but represent host association records verified through rearing trials. The following are coordinates of other sampled *Arnica* species: *A. cordifolia* (Utah, Daggett Co., Uinta

TABLE 1. Plant sample characteristics of *Arnica chamissonis* and rearing results for *Campiglossa snowi* from those samples taken from survey sites at the Kenai Peninsula, Alaska.

		Study sites		
Metric	Year	Seward Tracks	Salmon River	Nash Road
Number of plants sampled	2007	34	26	34
	2009	20	20	21
	2010	20	20	20
	2011	21	20	20
	2013	20	21	20
Total seed production per 20 plants	2007	19,099	16,417	10,140
	2009	6381	6447	7324
	2010	5358	5671	4716
	2011	4503	3161	4007
	2013	6021	8330	6800
Min–max seeds per capitulum	2007	54–192	52–131	45–159
	2009	46–119	53–126	34–142
	2010	41–142	42–121	47–112
	2011	52–117	41–114	52–142
	2013	37–107	50–115	48–144
Average seed per capitulum	2007	105.5	86.9	85.9
	2009	88.6	80.6	90.2
	2010	90.8	79.9	84.2
	2011	84.1	64.4	81.8
	2013	78.2	78.1	86.1
Average % seed damaged	2007	8.3	10.0	17.6
	2009	12.6	20.0	28.8
	2010	28.9	31.9	54.8
	2011	7.1	18.8	13.9
	2013	0.0	5.3	3.3
Average % capitulum infestation	2007	29.2	39.7	58.5
	2009	54.2	61.3	90.1
	2010	89.8	84.5	96.4
	2011	19.6	89.4	69.4
	2013	0.0	32.7	31.6
% Plant infestation	2007	52.9	84.6	97.1
	2009	85.0	85.0	100.0
	2010	100.0	100.0	100.0
	2011	30.0	94.4	90.0
	2013	0.0	95.2	71.4
Total reared *C. snowi*	2007	33	89	77
	2009	48	89	116
	2010	93	128	165
	2011	16	130	43
	2013	0	45	42

Mtns., 40.83796, −110.00060, 3106 m elevation, 5 August 2013) and *A. mollis* Hook. (Utah, Sanpete Co., Fairview Cyn., 39.57096, −111.30891, 3038 m elevation, 20 July 2013; Wyoming, Albany Co., Medicine Bow Mtn., 41.35332, −106.24796, 3245 m elevation, 9 August 2013; Oregon, Grant Co., nr Indian Peak, 44.75604, −118.71664, 1901 m elevation, 30 July 2014; Oregon, Hood River Co., Dufur Mill Rd., 45.39474, −121.5001, 1399 m elevation, 31 July 2014).

Pinned voucher specimens of tephritids were deposited in the insect collection (BYUC) at the Monte L. Bean Museum, Brigham Young University, Provo, Utah. Voucher specimens of *A. chamissonis* were deposited in the Stanley L. Welsh Herbarium (BRY) in the aforementioned museum. Plant vouchers have been databased and are accessible through the Southwest Environmental Information Network (SEINet 2009–2015) with the following herbarium catalog numbers: *A. chamissonis:* BRY41284, BRY41291, BRY41931, BRY40049, BRY40048, BRY47663, BRY114890, BRY38634, BRY32445; *A. mollis:* BRY41932, BRY622181, BRY622185, BRY

TABLE 2. Emergence of tephritid fly species from *Arnica chamissonis* locations additional to the 3 primary study sites.

Site	Coordinates	Elevation (m)	Specimens reared	Species reared
AK, Anchorage, Girdwood	60.94577, −149.16904	29	3	*Campiglossa snowi*
AK, Kenai Peninsula, Lowell Point	60.07039, −149.44212	10	8	*Campiglossa snowi*
AK, Kenai Peninsula, Homer	59.63972, −151.50459	3	3	*Campiglossa snowi*
AK, Kenai Peninsula, Tern Lake	60.53487, −149.54280	180	1	*Campiglossa snowi*
AK, Kenai Peninsula, Ninilchik	60.03962, −151.67183	37	1	*Campiglossa snowi*
AK, Matanuska-Susitina, Palmer	61.61391, −149.05296	134	2	*Campiglossa snowi*
WY, Park Co., Pelican Crk.	44.55653, −110.36163	2362	11	*Trupanea jonesii*
OR, Clackamas Co., Clackamas Lake	45.10080, −121.74295	1040	1	*Campiglossa snowi*
OR, Lake Co., Paulina Marsh	43.17627, −121.03632	1310	84	*Trupanea jonesii*
OR, Lake Co., Paulina Marsh	43.17627, −121.03632	1310	14	*Euarestiodes acutangulis*
OR, Lake Co., Paulina Marsh	43.17627, −121.03632	1310	13	*Tephritis leavittensis*
UT, Daggett Co., Uinta Mtns.	40.87836, −109.96466	2890	77	*Trupanea jonesii*
UT, Daggett Co., Uinta Mtns.	40.87836, −109.96466	2890	20	*Tephritis leavittensis*
UT, Daggett Co., Uinta Mtns.	40.87836, −109.96466	2890	3	*Trupanea nigricornis*

73170, BRY120510, BRY114886; *A. cordifolia:* BRY38653.

RESULTS

Between the 3 study sites on the Kenai Peninsula (2007–2011), capitula per plant varied from 3 to 9. Though not measured for height, plants in 2007 were observably larger than in subsequent years when the average number of flower heads was 4 per plant. The lowest average number of capitula per plant occurred in 2011 at 3 per plant across all sites. Seed production per capitulum ranged from 37 to 192 seeds with an overall average of 84 seeds across all 3 Kenai study sites and years (Table 1).

Though flower heads of *A. chamissonis* remained in plastic cups for 2 months, all flies emerged within 2 weeks of flower heads being placed in cups. The fruit fly *Campiglossa snowi* was the only fly species to emerge from the Alaska *Arnica* populations. This is the first host record for *C. snowi* with *A. chamissonis* and is the first published record of *C. snowi* occurring in Alaska, establishing a new northern range extension for *C. snowi* (Fig. 1). The only other insect that emerged from the Alaska sites was a metallic green parasitoid wasp in the genus *Pteromalus* (Pteromalidae, Hymenoptera). This wasp is a parasitoid of *C. snowi* and occurred in low numbers relative to the 1114 flies reared.

Capitulum infestation and seed damage varied by year at the 3 Kenai sites, with an apparent peak occurring in the year 2010 (Table 1). In 2013, average percent seed damage dropped below 6.0% at all sites, with no infestation occurring at the Seward Tracks site (Table 1). As would be expected, reared fly abundance mimicked infestation rates. Fly abundance and infestation rates gradually increased over several years, then were followed by a precipitous decline over several years. The average number of seed damaged per fly larvae from the Kenai Peninsula sites ranged from 7 to 18 seeds across all years and sites with an average of 12 (Table 1).

Flower heads of *A. chamissonis* collected and reared from locations other than our 3 primary study sites had mixed results of emerging taxa (Table 2). Additional sites from Alaska yielded only *C. snowi.* The only other investigated site exhibiting the host relationship between *A. chamissonis* and *C. snowi* was in Oregon at Mount Hood, the fly's type locality. Several other species of Tephritidae were reared from flower heads of *A. chamissonis* outside of Alaska (Table 2). *Trupanea jonesii* (Curran) was reared from *A. chamissonis* from Wyoming, Oregon, and Utah sites. *Trupanea nigricornis* (Coquillett) was reared from a Utah site, *Tephritis leavittensis* Blanc was reared from both an Oregon site and a Utah site, and *Euarestoides acutangulus* (Thomson) was reared from an Oregon site. It should be noted that specimens of *C. snowi* were reared from the flower heads of both *A. cordifolia* and *A. mollis* from locations in Utah, Wyoming, and Oregon.

DISCUSSION

Flower head production and seed yield varied greatly among years. Those differences are likely due to annual changes in environmental factors. Providing uniform nutrient and water resources to wild species under agricultural production systems could help mediate those differences, and agriculture models have been investigated for *A. chamissonis* (Cassells et al. 1999, Sugier 2007).

Host associations between *A. chamissonis* and tephritids have interesting biogeographical trends. The plant seems to only host *C. snowi* in its northern clime, particularly in Alaska where few other populations of suitable plants from Asteraceae are blooming concurrently and within proximity. The tephritid *C. snowi* occurs from California north to British Columbia, with additional records from Idaho, western Montana, and a single record from Colorado (Foote et al. 1993). The larvae of several species in the genus *Campiglossa* Rondani are known to feed on the developing seeds of *Arnica,* but nothing has previously been recorded from *A. chamissonis.* Previously, the only known *Arnica* host association for *C. snowi* was from *Arnica cordifolia* Hook. (Foote et al. 1993). The fruit fly *Trypeta flaveola* (Coquillett) has been reared from *A. chamissonis,* but it is a leaf miner rather than a seed predator (Frick 1971, Han and Norrbom 2005). We expect that *C. snowi* occurs across the entire range of *A. chamissonis* and will eventually be verified through future tephritid collections. Why other polyphagous tephritids were not reared from *Arnica* in Alaska is uncertain, but may have more to do with the biology of *C. snowi* and its ability to adapt to northern climates than with variations occurring between northern and southern genotypes of *A. chamissonis.* Polyphagous tephritids are able to utilize multiple plant species, and it would be unlikely that a specific *Arnica* genotype would deter them.

It is unusual that no other tephritid species was reared from the seed heads of 337 plants collected from the Kenai Peninsula of Alaska across 5 sample years spanning a 7-year period. This can partially be explained by the fact that Alaska falls outside the range of the common seed predators *T. nigricornis* and *T. leavittensis* (Foote et al. 1993). However, *T. jonesii* likely occurs in British Columbia, Canada, because it is found in northern Washington, and *E. acutangulus* has been recorded from Alberta and northern Saskatchewan (Foote et al. 1993). Both of these species are seed predators of *A. chamissonis. Neaspilota viridescens* Quisenberry occurs in Alaska and is known to feed on many different genera within Asteraceae (Foote et al. 1993) but was not reared from *A. chamissonis. Campiglossa albiceps* (Loew) occurs in Alaska and feeds on *Aster* spp., as does *Campiglossa dupla* (Cresson) on *Erigeron; Campiglossa clathrata* (Loew) on *Haplopappus* and *Senecio*; *Campiglossa farinata* (Novak) and *Campiglossa footeorum* (Novak) on *A. cordifolia, A. latifolia,* and *A. rydbergii* Greene; *Campiglossa genalis* (Thomson) on several genera; and *Campiglossa murina* (Doane) on *Haplopappus* (Foote et al. 1993).

A. chamissonis hosts at least 4 other tephritid species (some newly reported in this paper) across the more central part of the range. This is the first host record from a rearing trial for *T. leavittensis* on *A. chamissonis,* previously only thought to have a relationship with *Arnica diversifolia* Greene based on sweep net samples (Foote et al. 1993). This is also the first host record for *T. nigricornis.* Both *T. jonesii* and *E. acutangulus* have previously been reared from *A. chamissonis* (Wasbauer 1972). The genera *Trupanea* and *Euarestoides* are known to be polyphagous on many genera and species, but exclusive to Asteraceae. Foote et al. (1993) list 75 genera of plant hosts for *Trupanea* and 9 genera of plant hosts for *Euarestoides,* so it is not surprising to find them also on *A. chamissonis.*

Previous host records for *C. snowi* were limited to *A. cordifolia* (Foote et al. 1993) and *Senecio triangularis* Hook. (Novak 1974, Turner and McEvoy 1995). With the addition of *A. mollis* as a host in this paper, it is likely that most *Arnica* species can host *C. snowi.* The degree to which it feeds on the genus *Senecio* beyond the reported *S. triangularis* remains unknown, but the fly may not be as host specific as current records indicate. *Senecio* L. is a large genus with over 55 species recorded for North America (Barkley 2002) and an additional 64 former congeners now in the closely related genus *Packera* A. Love & D. Love (Trock 2002). Numerous seed heads from *Senecio,* including *S. triangularis,* were collected from the Oregon *A. chamissonis* sites where we successfully reared *C. snowi* from the *Arnica,* but not from *Senecio triangularis* or *S. jacobaea* L.

Though there was site-to-site variation within the Kenai Peninsula sites, the trends in seed damage from year to year showed synchronized increases and declines in fly abundance. The seed of an individual capitulum were never completely consumed, with the highest average damage per capitulum (54.8%) occurring at the Nash Road site in 2010 (Table 1). In contrast, Diehl and McEvoy (1989) reported that sometimes capitula of *S. triangularis* would be entirely consumed by *C. snowi.* Compared to studies of fly damage in other composites (Johnson 2008), the number of *A. chamissonis* seeds damaged per fly may be high in comparison. It appears that the larvae of this species are highly mobile and feed throughout the flower head, damaging numerous seeds while consuming few. Capitulum damage, while primarily associated with developing seed, was not always the case. In some rare instances, larvae fed on and pupated within the floral parts above the seed, leaving the ovules and seed undamaged. This phenomenon, however, is not typical among seed-feeding tephritids (Headrick and Goeden 1998).

CONCLUSION

It is clear that *A. chamissonis* hosts a number of seed predators and that *C. snowi* has an affinity for multiple species of *Arnica.* Considering the potential value of *A. chamissonis* for roadside reclamation and pharmaceutical use, seed pest management is warranted. As is often the case, native species of wild-collected seed contribute a significant portion toward seed availability for the industry. While reducing fruit fly pests in wild populations of *Arnica* is not practical, it could greatly increase seed yields for plants brought under cultivation. The agricultural production of seeds for the reclamation industry and the harvesting of seed heads for the pharmaceutical industry would both benefit from programs that manage seed-predating fruit flies.

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