CAN CONSERVATION BIOCONTROL OF WHEAT STEM SAWFLY BE IMPROVED? CONTRIBUTIONS OF SUPPLEMENTAL NUTRITION TO LONGEVITY, EGG LOAD, AND EGG VOLUME OF *Bracon cephi* and *B. lissogaster*

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DEDICATION

For those who are committed to a better world and envision a more innovative and sustainable way forward in agriculture.

Eternity is in love with the productions of time
William Blake

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ABSTRACT

Wheat stem sawfly (WSS), *Cephus cinctus,* is a major pest of wheat, causing losses that exceed $350 million annually across the Northern Great Plains. Two native parasitoids, *Bracon cephi* and *B. lissogaster,* suppress *C. cinctus* populations in wheat fields, where the immatures feed on and kill *C. cinctus* larvae. The success of natural enemies is linked to access to supplemental food in the field, which increases their life span and benefits their reproductive parameters. To assess the benefits that supplemental nutrition might have on *B. cephi* and *B. lissogaster*, we reared adult females on carbohydrate-rich diets combined with and without amino acids, with water and water plus amino acids as controls. We also conducted greenhouse experiments with the non-native, warm-season cover crop cowpea, *Vigna unguiculata*, as an extrafloral nectar source for parasitoids. Cages containing individual females were placed on living plants enclosing either cowpea inflorescence stalk extrafloral nectar (IS-EFN) or the leaf stipel extrafloral nectar (LS-EFN), with a supply of water as the negative control and buckwheat nectar as the positive control. In both lab and greenhouse experiments, females were observed daily to assess longevity, while egg load and volume were assessed 2, 5, and 10 days after placement. Results show that both species increased longevity when provided carbohydrate-rich food. *B. cephi* enhanced egg load and volume with carbohydrate-rich diets, and the addition of amino acids tending to benefit these parameters. Results show that IS-EFN increases longevity in both parasitoids. *B. lissogaster* kept constant egg load and volume, while *B. cephi* increased reproductive parameters with IS-EFN. These native braconid parasitoids are unfamiliar with non-native cowpea plants. Hence, we tested their attraction to cowpea volatiles, where positive responses were observed. Our results show that supplemental nutrition greatly benefits *B. cephi* and *B.* lissogaster females, with cowpea IS-EFN improving their longevity and reproductive parameters. Therefore, we suggest that cowpea has potential to be considered as a food supplement crop in conservation biocontrol programs to reduce WSS populations.

CHAPTER ONE

LITERATURE REVIEW

Wheat Stem Sawfly

Wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), is an opportunistic and adaptive native species that is the major pest of wheat in the Northern Great Plains of North America, particularly Montana, Idaho, Wyoming, Nebraska, Colorado, plus North and South Dakota (Ainslie, 1920; Irell and Peairs, 2011; Lesieur et al., 2016). Wheat stem sawfly was also reported on the Canadian Prairies, especially in Manitoba, Saskatchewan, and Alberta (Beres, et al., 2011a; Weiss and Morrill, 1992). Wheat stem sawfly has repeatedly affected North American wheat production since its cultivation began, first reported damaging wheat in 1896 in parts of Saskatchewan and Manitoba, Canada (Weiss and Morrill, 1992). The damage to wheat is caused by larval feeding and the subsequent cutting and lodging of the wheat stem (Ainslie, 1920; Bekkerman and Weaver, 2018). This affects the growing wheat plants by reducing kernel weight and the protein content of the grain, in most varieties (Holmes, 1977).

Life Cycle

The female WSS typically deposits a single egg in the stem per visit, but females do not avoid infested plants and lay multiple eggs in a single stem (Buteler et al., 2009). The oviposition happens in mid-May to mid-June in Montana (Fulbright et al., 2011), and in rare cases, the females can lay two eggs per stem during their visit, which can be a response to taller wheat stems that provide a greater target size or an increased oviposition stimulus (Buteler et al., 2009).

WSS females lay eggs during wheat stem elongation, and this process does not cause significant injury to the plant (Wallace and McNeal, 1966). Approximately seven days after oviposition, the larva emerges from the egg inside the stem lumen (Ainslie, 1920), where it starts to feed and consume the parenchyma and vascular tissues of the plant, reducing its photosynthetic capacity (Ainslie, 1920; Macedo et al., 2005). The larvae are cannibalistic, and when there is more than one individual living in the same stem, it kills the other larvae and eggs, becoming the only survivor (Ainslie, 1920; Buteler et al., 2009; 2015). In the final instar, the surviving larva descends to the base of the stem to prepare for overwintering by cutting a neat v-shaped groove in the interior of the stem wall (Ainslie, 1920; Wallace and McNeal, 1966). The damage caused by the larva makes the base of the stem very weak and brittle, as a consequence, it eventually breaks, especially in windy conditions. The remaining lower part of the stem is called a stub and it will be used as a winter chamber by WSS larvae in diapause (Ainslie, 1920; Holmes and Peterson, 1960).

After overwintering, the larva develops into pupa in late May when temperature starts to rise (Holmes, 1977), and this stage lasts about 20 days (Fulbright et al., 2011). The timing of emergence is influenced by ambient temperature and relative humidity (Perez-Mendoza and Weaver, 2006), where males usually emerge before the females, and they are notably smaller (Ainslie, 1920; Holmes, 1979). Copulation occurs immediately after emergence, with the fertilized eggs generating diploid females and unfertilized eggs producing haploid males, and the adult lifespan of both sexes range from five to eight days (Wallace and McNeal, 1966). Different than for larvae, WSS adults were reported feeding on nectar at the field (Rand et al., 2019, Wallace and McNeal, 1966). Their lifespan can increase with supplemental nutriton, such as buckwheat nectar, however, an increase on egg deposition rates has not been reported (Rand et al. 2019). This is likely due in part to a fixed egg number at the time of adult emergence from the stub, since these females are proovigenic (Jervis et al. 2001).

Management

WSS causes damage in both spring and winter wheat (Ainslie, 1920; Morrill et al., 1998; Morrill and Kushnak, 1996) and has caused repeated economic losses in wheat crops in North America. More recently, according to Bekkerman (2014), the losses caused by WSS in Montana wheat crops have ranged from $40 to $80 million annually from 2008 – 2012. Key management tactics for WSS are described below.

Cultural control During the early 1900s, cultural control practices were suggested to control WSS. These included early harvesting, tillage (deep plowing), destruction of host plant reservoirs, and burning the stubble that was not turned over in the fall (Beres, et al., 2011a, 2011b). However, most of these techniques were not effective in controlling WSS populations and had negative effects on the soil and natural enemies of the WSS (Beres et al., 2011a; Runyon et al., 2002). As first reported by Ainslie (1920), burning the crop residue is inefficient because larvae did not suffer noticeable injury from the heat produced when the stubble burns.

Some other techniques for cultural control have may have had better results, such as trap crops (Morrill et al., 2001, Shelton and Badenes-Perez 2006). In addition, crop rotation with non-cereal crops might be beneficial to WSS control, while also improving wheat yield and grain protein (Beres, et al., 2011a). Delayed planting is another alternative; however, it can negatively impact wheat yield due to lower availability of soil moisture later in the season. (Morrill and Kushnak, 1999).

Chemical control The WSS life cycle makes it difficult to develop an insecticide that does not prejudice grain safety or kill other insects that could prey on WSS larvae (Beres, et al., 2011a). The efficacy of insecticidal applications has been investigated in several studies, but because of negative results, only a few findings were published (Beres et al., 2011a). Heptachlor was the only tested insecticide that was effective against WSS larvae in an early report (Holmes and Peterson, 1963). Considerable mortality only occurred early in the larval stage. In early development, the larva stays in the lower internodes of the stem, and this is the region where heptachlor is present in bigger concentrations (Holmes and Peterson, 1963). However, this insecticide's registration has not been renewed in the USA since 1988 because of its soil persistence (Anonymous, 1997).

WSS spends most of its life cycle inside the wheat stem, making it very unlikely that pesticides can be developed to effectively kill the larvae without compromising grain safety or killing natural enemies of the WSS (Beres et al., 2011a). However, the systemic, granular organophosphate insecticide phorate or 'Thimet 20-G®' is effective against WSS in treated fields (Peairs et al., 2014), and was also registered for use post crop emergence against WSS larvae in Montana wheat by the Montana Department of Agriculture. However, this insecticide poses potentially unacceptable health and environmental risks (Lerro et al., 2015) and has a long preharvest interval of 85 days (Mahajan et al., 2006; Portman et al., 2018). In addition, its toxicity might negatively affect the parasitoids that specialize on WSS larvae (Varella, 2016).

For these reasons, use by growers was very limited and the 'Special Local Need' registration for use against WSS larvae in wheat in Montana was not renewed.

Host-plant resistance Stem solidness is a qualitative trait controlled by recessive genes and is the most used type of host-plant resistance against WSS. The genes involved in pith development are controlled by photoperiod and light intensity during stem elongation, and are inhibited during cloudy or shady conditions, limiting overall adoption of this type of management (Beres et al., 2011a; Eckroth and McNeal, 1953; Holmes, 1984). Solid-stem cultivars often have lower grain yields (Beres et al., 2011a), but one alternative to offset this outcome is to plant a blend of both solid-stem and hollow-stem cultivars in the same field (Beres et al., 2009).

Attractiveness of the host plant is another important mechanism to manage this pest. WSS females prefer to oviposit in cultivars that have a greater amount of (*Z*)-3-hexenyl acetate, an attractant volatile compound (Weaver et al., 2009). Thus, cultivars that release lesser amounts of this compound are likely to be less attractive to WSS females, and consequently fewer eggs are going to be laid in these cultivars. In addition, infestation by WSS induces quantitative changes in the production of several wheat volatiles (Peck, 2004), and these volatiles can play an important role in attracting the parasitoids of the WSS. Pérez (2009) used synthetic compounds to evaluate the volatiles released by wheat plants under WSS infestation, showing that both *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae) display antennal and positive wind tunnel responses to these compounds.

Biological control Only two parasitoid species, from a larger complex in wildland grasses, are known to use WSS larvae in wheat stems, *B. cephi* and *B. lissogaster* (Davis, 1955; Morrill et al., 1994; Somsen and Luginbill, 1956). Parasitism occurs when the WSS larvae are feeding inside wheat stems during the growing season (Holmes et al., 1963). In Montana, most of the WSS larval mortality is caused by these two parasitoids and it augments host plant resistance, which is the other major source of mortality (Buteler et al., 2015).

The use of other biological control agents has been attempted in Montana and North Dakota with several releases of the exotic parasitoid *Collyria calcitrator* (Gravenhorst) (Hymenoptera: Ichneumonidae), but these were unsuccessful, and this species did not become established (Davis, 1955). The same outcome was evident for earlier attempts using the two exotic species *Collyria coxator* (Villers) (Ichneumonidae) and *Bracon terebella* (Braconidae) (Smith, 1931). Another more recent project involved the species *Collyria catoptron* (Wahl) (Ichneumonidae), which parasitizes *Cephus fumipennis* Eversmann in eastern Asia. This species was imported for quarantine evaluation of its capacity to kill WSS (Rand et al., 2016). Even though C. *catoptron* recognizes, paralyzes, and oviposits on larval WSS, it is unable to complete its development using these larvae, providing clear evidence that it is unlikely that this parasitoid could be used to manage WSS populations in western North America (Rand et al., 2016).

Braconid Parasitoids

Biological control by *B. cephi* and *B. lissogaster* can be very effective in suppressing WSS populations. In comparisons of Montana wheat crops, it was observed that parasitism accounted for as much as 34% of WSS larval mortality, where 12% of this mortality could not be replaced by another mortality factor (Buteler et al., 2015). These parasitoids are i) sympatric, meaning they exist in the same area at the same time; ii) idiobionts, because adult females immobilize their hosts, and iii) ectoparasitoids, because they feed on the host from the exterior (Runyon et al., 2001). Both species are bivoltine, having two generations per year, but when there is early maturity of wheat caused by weather conditions (extremely dry or hot), these parasitoids have only one complete generation per year (Holmes et al., 1963).

Bracon cephi and *B. lissogaster* cause two related positive effects on wheat crops. First by paralyzing the WSS larva, making it unable to feed inside the wheat stem, and as a consequence, physiological yield loss is curtailed (Bekkerman, 2014; Buteler et al., 2008). Second, the parasitoids eventually kill the WSS larva, making it impossible for the larva to cut the stems or cause damage in subsequent wheat crops. (Buteler et al. 2008, Morrill et al., 1998, Nelson and Farstad 1953, Peterson et al., 2011).

Bracon cephi

The eggs that are laid by the first generation in June or July will hatch and feed on WSS larvae, become pupae, and emerge as second-generation adults (Holmes et al., 1963). The second-generation adults will oviposit less than a month later in July or August, and the larvae from these eggs will overwinter as prepupae inside the stems after feeding on WSS larvae (Holmes et al., 1963). The emergence of the first generation of *B. cephi* and adults of WSS is synchronous, but during the first 12 to 21 days of flight the parasitoids will not oviposit (Holmes et al., 1963; Nelson and Farstad, 1953). This period is called “pre-oviposition”, and the exact reason why it happens is unknown. However, there is speculation about possible causes: i) females need this time to restore nutrient reserves from overwintering time to complete egg maturation (Nelson and Farstad, 1953); ii) parasitoid larvae need to wait for host WSS larvae to become sufficiently large to fully accommodate larval parasitoid development (Holmes, 1963). As opposed to the first generation, the second-generation females oviposit as soon as they emerge (July–August), and the reproductive success of this generation is linked to how late in the season the first-generation females are able to oviposit (Holmes et al., 1963).

For oviposition to occur, the female must locate the infested stem containing the WSS larva using specific wheat volatiles and vibrations made by the WSS larva when moving or feeding from the stem (Mankin et al., 2004; Pérez, 2009). Adult female *B. cephi* can have six to ten mature eggs in their ovaries and oviposit two to four of these each day (Nelson and Farstad, 1953). When a female finds the host, she straddles the stem at the point where she will insert her ovipositor. After inserting the ovipositor, she injects venom to immobilize the WSS larva and only after that will she deposit an egg near the larva.

A parasitoid larva emerges from the egg after one or two days, then finds and attaches itself to the immobile WSS larva and starts to feed on all tissues except the integument (Holmes et al., 1963; Nelson and Farstad, 1953). After ten days the host is consumed and the parasitoid larva, already developed, spins a cylindrical cocoon inside of the stem, where it pupates and enters diapause. Normally cocoons of the first generation are loosely woven, while cocoons of the second generation are more tightly woven (Nelson and Farstad, 1953). To survive overwintering, *B. cephi* produces a high concentration of glycerol that depresses the freezing point of the hemolymph, allowing survival under very cold conditions, and if the hemolymph does freeze, the tissues are protected from injury caused by ice crystals by limiting crystal size (Salt, 1958).

Bracon lissogaster

Bracon lissogaster has a very similar life cycle to *B. cephi* but has a shorter pre-oviposition period of only six to eight days after emerging from the overwintering stem (Somsen and Luginbill, 1956). The females can lay one to four eggs in each host and this species is thus gregarious. After six to eight days, larval development is completed. When there is more than one larva feeding on the host, development is more rapid because of reduced food availability. Under these conditions the larvae still develop completely, but they are smaller (Somsen and Luginbill, 1956).

After completing development, *B. cephi* and *B. lissogaster* adults emerge by chewing a hole through the cocoon and stem and move to the exterior surface of the stem before taking flight. Males emerge first and live about 10 to 14 days, while females typically live for approximately four weeks (Nelson and Farstad, 1953).

Nutrition and Parasitoid Success

Floral vegetation provides sugar resources that are important for parasitoid survival and can improve their efficiency as biological control agents (Heimpel and Jervis, 2005; Russell, 2015), therefore, flower nectar can be an important resource on conservation biological control (Munir et al., 2018). Interestingly, parasitoids have the ability to use visual and olfactory cues to learn and modify their behavioral responses (Lewis et al., 1998), making it possible for them to use plant attractiveness parameters, such as volatile compounds and flower color, to find nectar (Belz et al., 2013; Wäckers, 2004).

Carbohydrate-rich food like nectar is an important energy source for beneficial insects (Wäckers, 2004; Winkler et al., 2005). It can increase longevity, fecundity, and rates of parasitism in parasitic hymenopterans (Heimpel et al., 1997; Lee et al., 2004; Lee and Heimpel, 2008; Lewis et al., 1998; Tunçbilek et al., 2012), and parasitoids that feed more often tend to perform better as natural enemies of crop pests (Azzouz et al., 2004). According to Lee et al. (2004), parasitoid longevity increased when buckwheat nectar and aphid honeydew were available, with buckwheat nectar doubling parasitoid longevity when compared to honeydew. Parasitoids have increased fitness when feeding on honeydew, showing the importance of carbohydrate-rich diet in these organisms (Tena et al., 2018). The literature indicates that sucrose can play an important role in parasitoid reproductive success and longevity (Reis et al., 2019; Siekmann et al., 2001).

Regarding *B. cephi and B. lissogaster*, it is important to emphasize that they feed on WSS during the immature stage (Holmes et al., 1963; Nelson and Farstad, 1953), but to this date adults have not been reported to feed on WSS larvae. Therefore, adult food supplementation can play an important role in these parasitoids' biology in addition to the nutrients acquired during their larval stage. Parasitoids developing in large wheat fields are not likely able to acquire supplemental nutrition. Interestingly, Rand and Waters (2020) noticed that buckwheat nectar (corroborating Reis, 2018) and aphid honeydew benefited braconid parasitoids in their longevity when compared to nectar from sunflower and coriander. Reis et al. (2019) showed that sucrose had a positive effect on reproductive success of the WSS parasitoids, where *B. cephi* and *B. lissogaster* had increased longevity and egg load, and *B. cephi* also had enhanced egg volume. The same authors noticed that the benefits did not differ between overwinter and summer generations, suggesting that both species are well adapted to seasonal weather changes and can exploit available extrafloral resources irrespective of timing.

Parasitoid life history is another factor to consider in conservation biological control, specifically whether they are pro-ovigenic or synovigenic. This characteristic plays an important role in the influence of floral resources on longevity and fitness (Jervis et al., 2001). *Bracon cephi* and *B. lissogaster* are both synovigenic, so they have both immature and mature eggs before oviposition begins (Flanders, 1950), and thus, can potentially benefit from nectar availability by increasing longevity and fecundity. As a consequence, they increase their success as biological control agents (Jervis et al., 2008; Manandhar and Wright, 2016a).

Nectar Sources and Habitat Manipulation

Nectar is a carbohydrate-rich fluid supplied from phloem that contains amino acid compounds and is dominated by the sugars: glucose, fructose, and sucrose. It mediates interactions between plants and pollinators or natural enemies, and its daily secretion depends on air temperature and humidity (Brandenburg et al., 2009; De La Barrera and Nobel, 2004). Adgaba et al. (2017) demonstrated that optimal ambient temperatures for secretion differ by plant species, where plants that are adapted for hot climatic conditions seem to have their peak nectar secretion positively correlated with ambient temperature. Therefore, nectar secretion patterns differ for different plant species (Adgaba et al., 2017). However, the secretion of extrafloral nectar seems to be mostly diurnal, with peak secretion occurring during the first 2 h after dusk (Heil et al., 2000). This can benefit parasitoids because of availability of droplets when they tend to be active during sunny periods of the day (Winkler et al., 2009). Moreover, nectar production can also be influenced by the presence of consumers. The plant species *Macaranga tanarius* (Euphorbiaceae) increased nectar production when consumers, such as ants and other insects, were present and feeding (Heil et al., 2000).

The attraction of nectar as a food resource for insects is related to its components and sucrose ratio, which can change across and within plants (Jervis et al., 1993). Similarly, consumers have individual preferences for nectar composition due to this varying in rate of sugar to amino acid contents of the nectar (Escalante-Pérez and Heil, 2012). The ratio of nectar sugars is often correlated to pollinator needs (Pamminger et al., 2018). In the case of bees, the optimal concentration of sugar ranges 35-65%, which is the required to keep bee populations healthy (Kim et al., 2011; Pamminger et al., 2018). In addition, the sugar concentration in nectar is positively related to fitness, which serves as an indicator of nectar quality (Brodschneider and Crailsheim, 2010; Vaudo et al., 2015, 2016). Interestingly, in the same plant, the composition of floral and extrafloral nectar can differ. Baker et al. (1978) analyzed nectar from different plant species, and noticed that extrafloral nectars have more cysteine, lysine, asparagine, and tyrosine when compared to floral nectar. They suggested that these differences are related to the functions of extrafloral nectar feeding natural enemies, while floral nectar is consumed by pollinators.

When assessing the suitability of non-host food sources, not only the quality and quantity of nectar need to be considered, but also the plant attractiveness and accessibility by natural enemies without benefitting pest insects (Wäckers and van Rijn, 2012). Nectar access by parasitoids is influenced by flower morphology (Patt et al., 1999; Wäckers, 2004), mouthpart morphology, and overall body size (Heimpel et al., 1997). Therefore, it is crucial to match quality food sources and accessibility with the behavioral and morphological characteristics of a specific parasitoid species for successful biological control (Olson et al., 2005). Hymenopteran parasitoids with generalized mouthparts prefer to feed from more "open" nectar sources (Gilbert and Jervis, 1998; Vattala et al., 2006), such as the surfaces of extrafloral nectaries or nectaries covered by a tubular corolla (Jervis, 1998). Stapel et al. (1997) showed that some parasitoid species are highly attracted to extrafloral nectaries and these parasitoids perceive nectar more readily than sucrose droplets or honeydew. In addition, factors such as ambient temperature and humidity can influence the ability of some insects to feed on nectar because high temperatures and low humidity can lead to water evaporation, causing nectar crystallization (Adgaba et al., 2017; Corbet et al., 1979). However, parasitoids are less likely to suffer diet restrictions due to these conditions and can typically feed on highly concentrated sugar sources (Winkler et al., 2009).

Providing flower species that permit easy access to nectar by parasitoids is a beneficial strategy in biological control, which is known as habitat manipulation or ecological engineering (Gurr et al., 2004). Habitat manipulation can preserve natural enemies present in the ecosystem and make the management of pests more effective (Kumar et al., 2013). Floral vegetation can provide sugar resources that are important for parasitoid survival and efficiency as biological control agents (Heimpel and Jervis, 2005; Russell, 2015), and thus, floral and extrafloral nectar resources should be considered when implementing or improving conservation biological control techniques (Munir et al., 2018; Pate et al., 1985). It is also important to verify if the chosen nectar source does not nutritionally benefit targeted pests. For example, buckwheat has exposed nectaries (Winkler et al., 2010), which could make it a good nectar source candidate, but study by these same authors revealed that nectar access increased the number of eggs and larvae of the cabbage pest *Pieris rapae* L. (Lepidoptera: Pieridae). Therefore, buckwheat is inadequate in this system. Conversely, Rand et al. (2019) reported that in the presence of buckwheat females of WSS had increased longevity, but this did not alter egg deposition rates, and thus, was not likely to benefit this pest due to its fixed egg number at the time of adult emergence (Jervis et al. 2001; Rand et al., 2019).

The use of entomophilous plant strips in habitat manipulation can enhance nectar and pollen availability, with wildflower strips performing better than grass and spontaneous vegetation strips (Santos et al., 2018a). In this study, the authors noticed that wildflower strips attract natural enemies, such as syrphid flies. The same benefit was observed in a sugarcane field surrounded by forest fragments in Brazil (Santos et al., 2018b). According to the authors, forest fragments provide more variety of nectar and extrafloral nectar, as well as branches and litter for cover. Consequently, there is an increase in predatory and omnivorous ant communities. Equally, when examining the benefits to parasitoids, a study by Berndt and Wratten (2005) showed that parasitoid males and females increased their longevity when flower strips were present at the field, which also increased female lifetime fecundity. These beneficial effects are possible because there is a boost in nectar quality when there is an increase in wild plant community in an area (Pamminger et al., 2018). Moreover, wildflower strips can benefit the insect community composition of a determined area, such as predators and parasitoids of crops pests, and other species that play a role in decomposition and nutrient cycling (Grass et al., 2016).

In crop rotation systems, annual flower strips can be an important resource for natural enemies. A targeted selection of flowers can play an important role in providing food resources to natural enemies during the growing season, improving natural enemy abundance in the field (Tschumi et al., 2014). Wildflower plants offer resources for flower visitors at the late flowering season, when crops are no longer flowering and food sources are scarce (Blitzer et al., 2012; Riedinger et al., 2015). In addition, perennial plants provide structural and food resources for natural enemies, such as pollen, nectar, and shelter (Tschumi et al., 2014). Interestingly, a study by Tschumi et al. (2015) showed that the presence of flower strips adjacent to winter wheat decreased pest populations and increased natural enemies, and as a consequence, decreased damage of crop plants. Similarly, when the strips were present in potato fields, there was a decrease in aphid density due to an increase in natural enemies, such as syrphid flies and lacewings (Tschumi et al., 2016). They also observed an increase on eggs being laid by this natural enemies, indicating the efficacy of this strategy on crop fields.

Cowpea

Legumes are well-known for being one of the flowering plants that have root nodules with the bacteria *Rhizobia* spp. (Doyle, 2001; Billault-Penneteau et al., 2019; Gonzalez-Rizzo et al., 2018; Zahran, 1999). These bacteria capture nitrogen from the atmosphere and convert it into other nitrogenous compounds that can be used by the plant, such as ammonia and nitrates

(Zahran, 1999). Therefore, there is limited need to use nitrogenous fertilizers in soils where legumes are present (Doyle, 2001; Zahran, 1999). Some examples of leguminous plants are soybean, pea, peanut, lentil, and different kinds of beans, including cowpea (Udvardi and Poole, 2013).

Cowpea, *Vigna unguiculata* (L.) Walpers, is a member of the family Fabaceae, genus *Vigna*, and section *catiang* (Pasquet, 1993, 1997, 1998, 1999). The species *unguiculata* can be divided into five different subspecies (*unguiculata*, *sesquipedalis*, *textilis*, *biflora*, and *melanophthalmus*), where *unguiculata* is the commonly cultivated group and *textilis* is used for fiber production in some places in Nigeria (Boukar et al., 2018). Some of its common names include crowder pea, black eyed pea, southern pea, field pea, catjang and yard-long bean, and are known internationally as caupi, lubia, niebe, coupe, or frijole (Clark, 2012; Sheahan, 2012; Quinn and Myers, 2002). Even though its origin is uncertain, ancestral cowpea forms are not encountered outside Africa, suggesting that these arose in Africa (Freire Filho, 1988).

The plant can have erect, suberect or spreading stems (Duke et al., 1981). Some other characteristics include trifoliolate leaves on long petioles (5-15 cm), and an axillary inflorescence that can be a raceme or long peduncle, with corolla colors ranging from white to violet, typically 2-3 cm in diameter (Duke et al., 1981). The pods reach commercial maturity (fresh pods) eight to ten days after anthesis, and subsequently start to accumulate fibers and lose tenderness and juiciness (Karapanos et al., 2017). When compared to other legumes, cowpea pods require a shorter period of time to achieve commercial maturity and need fewer inputs (Karapanos et al., 2017).

Statistics from the FAO show that from 1994 to 2019 about 95% of the world production of cowpea was from Africa, with the biggest productivity being from Nigeria, Niger, and Burkina Faso (FAOSTAT, 2020). In the US, cowpea is the most productive heat-adapted annual legume of agronomic importance being grown (Abate et al., 2011). In addition, it has socioeconomic importance in parts of Brazil and Africa for being one of the most important protein sources in these areas (Akinyele and Akinlosotu, 1987; Carvalho et al., 2012), where it is consumed alone or combined with other cereals to increase protein availability (Akinyele and Akinlosotu, 1987). The fresh pods contain glucose, fructose, sucrose, maltose and protein, being classified from moderately high to rich in protein content (Karapanos et al., 2017). In addition, it is also an important source of vitamins, minerals, and fiber (Phillips et al., 2003). Its seeds contain 23-25% protein, 50-67% carbohydrates (Devi et al., 2015), vitamins and minerals that can have anti-inflammatory, anticancer, and antidiabetic properties (Duodu and Apea-Bah, 2017).

Legumes are also an important nutritional source for insects, such as foraging honey bees that consume legume nectar (Furgala et al., 1958). In addition to nectar, its pollen also benefits insect nutrition. For example, the pollen of *Vicia faba* L. (Fabaceae), contains 18 different amino acids, including the most essential amino acids required for honey bee nutrition (Cook et al., 2003). In the case of cowpea, it is known that its nectar attracts many insects, including butterflies, house flies, and honey bees (Ige et al., 2011). Honey bees are highly attracted to cowpea pollen and nectar (Fohouo et al., 2009), and even though cowpea is a self-pollinating plant (Ige et al., 2011), this interaction favors both cowpea and honey bees. Honey bees contribute to cowpea pollination, while cowpea provides resources that are important to maintain the nutritional needs of the honey bee colony (Fohouo et al., 2009). In addition, pollinators such as domestic bees, bumble bees, anthophorids, melipones and hummingbirds benefit cowpea productivity, whether it is auto- or cross-pollination of visited flowers, increasing the number of seeds per pod by 17.4% and the number of pods by 11.2% (Vaz et al., 1998).

Cowpea Extrafloral Nectaries Cowpea has two different types of extrafloral nectaries, i) at the stipels of trifoliate leaves, at the point of attachment of the leaflets to the petiole of each trifoliate leaf, and ii) at the inflorescence stalk, between a pair of flowers bodies (Kuo and Pate, 1985). The stipel extrafloral nectaries are papillae of widely-spaced trichomes borne on a relatively unspecialized, stomata-free epidermis, and consist of a circular area (1-2 mm diameter) of widely-spaced multicellular secretory trichomes at the abaxial face of the stipel. Conversely, the inflorescence extrafloral nectaries consist of a large elliptical mound of tissue, with four to eight subunits of secretory tissue with an individual supply of phloem. The cells of these secretory units further separate as they mature, and each mature secretory cell has many small spherical protein bodies and one to three large paracrystalline bodies (Kuo and Pate, 1985).

The composition of nectar from these two extrafloral nectaries are different between them and also differ from the phloem sap (Pate et al., 1985). The stipel nectar has lower amino acid-sugar balance, and less nitrogenous solutes when compared to the inflorescence-stalk nectar. Nevertheless, the phloem sap is richer in amino acids and ureides, suggesting that a selective retention of nitrogenous solutes occurs when nectar is being formed (Pate et al., 1985). However, both extrafloral nectaries are thought to produce nectar with high sugar concentrations (sucrose, fructose, glucose), with equal parts by weight of these three different sugars and a total sugar concentration up to 70% (Pate et al., 1985).

Buckwheat

Wild type, ancestral buckwheat originated in the southwest of China and was cultivated in all East Asia, being spread to Europe around 1200 to 1300 AD (Zhou et al., 2018c). It was first cultivated in America after the 17th century, and currently it is grown in almost all countries that cultivate grain crops (Krochmal, 2011; Zhou et al., 2018c). Buckwheat, *Fagopyrum esculentum* Moench (Polygonaceae), is an annual pseudo-cereal and some common names include fat hen, French wheat, willow-wand, heathen corn, Tartar corn, Greek corn, and Saracen corn, as well as brank, beech wheat, and heath corn (Krochmal, 2011). The plant is 60-150 cm in height (Picard and Tsukamoto, 2017) and some other characteristics include long and pointed leaves, hairy stems that can be green or red, and brown seeds that are triangular in shape that can be smooth or rough (Campbell, 1997; Zhou et al., 2018a, 2018b). The dimorphic flowers are usually white, but can be pink-green, green-white, or rose, and each plant display either long styles and short stamens (pin flowers) or short styles and long stamens (thrum flowers). Usually, the same flower types cannot pollinate each other. However, it is possible to find plants with short-style and short-stamen types in common buckwheat, which can then achieve self-pollination (Campbell, 1997; Krochmal, 2011; Marshall, 1969). Its seeds are highly nutritious and are rich in proteins, amino acids, vitamins, minerals, fibers, lipids, polyphenols, and rutin (Kim et al., 2006; Zhou et al., 2018b). Therefore, it is used for animal and human food, and its flour is widely used in North American dishes (Krochmal, 2011).

Common buckwheat is an indeterminate crop that begins flowering 35-45 days after planting in warm soil (Picard and Tsukamoto, 2017). Buckwheat is sensitive to freezing temperatures and must be sown after the risk of frost is over. Another advantage that buckwheat offers as a cover crop is the capacity for suppressing weed growth due to its rapid growth rate (Björkman et al., 2008; Pilipavičius et al., 2009) and, consequently, reducing aerial biomass and root growth of different weeds, such as barnyard grass, goosefoot, and redroot pigweed (Gfeller et al., 2018). This is possible because, when cultivated with other weeds, buckwheat changes its root exudates. (Gfeller et al., 2018).

Buckwheat produces large volumes of nectar, which makes it a commonly used flowering resource in conservation biological control (Fiedler et al., 2008) in vegetable farms (Lavandero et al., 2005; Lee and Heimpel, 2005; Lee et al., 2006), and vineyards (Berndt et al., 2006). In addition, its corolla aperture is broad enough for parasitoids to insert their head and feed on the nectar (Vattala et al., 2006). The production of nectar occurs in glands at the base of the ovary, and its secretion is constant during daylight periods (Cawoy, 2006). Nectar secretion is also influenced by the growth stage of the plant and the position of the inflorescence at the stem, where flowers in upper inflorescences have the highest nectar productivity during the peak flowering (Cawoy et al., 2008). The nectaries are eight hook-shaped protrusions at the receptacle between the stamens, and at the ventral face of the hook it has unicellular trichomes through where nectar is secreted (Cawoy et al., 2008). In addition, the multilayered nectary parenchyma is supplied with water and nutrients from phloem and xylem.

The nectar contains sucrose, glucose, and fructose, and because it is sucrose dominant, it is considered a good nectar source for insects (Tompkins et al., 2010; Vattala et al., 2006). In addition, buckwheat attracts parasitoids (Lee and Heimpel, 2005), wild pollinators (Cawoy et al., 2009), syrphid flies (Vattala et al., 2006), and honey bees (Cawoy et al., 2006; Hogg et al., 2011) under field conditions. Interestingly, (Cawoy et al., 2006) observed that honey bees visited more often and spend more time in thrum flowers when compared to pin flowers. The authors explanation include that thrum flowers offered nectar in higher quantity and quality. In addition, buckwheat nectar improves the sex ratio of parasitoids (Berndt et al., 2002), as well as longevity, egg load, and number of offspring (Irvin et al., 2014). Reis (2018) first reported that buckwheat nectar increases longevity, egg load, and egg volume in *B. cephi*. While Rand and Waters (2020) also noticed that *B. cephi* increases longevity when fed buckwheat nectar. Rand et al. (2019) compared the implications of WSS feeding on buckwheat nectar, canola nectar, white mustard nectar, aphid honeydew, honey, and sucrose. Their results show that WSS increases its longevity when feeding on buckwheat nectar but did not boost egg deposition rates. Even though WSS is proovigenic and cannot increase its egg load based on food supplementation, increasing its longevity could enhance time for oviposition and infestation rates, however, it is not the case when WSS fed on buckwheat nectar (Rand et al., 2019).

Even though buckwheat has many positive qualities, the USDA Natural Resources and Conservation Service suspended the use of buckwheat in rotation with or adjacent to commodity wheat production in Colorado, Kansas, Idaho, Minnesota, Montana, Nebraska, North Dakota, Oregon, South Dakota, Washington, and Wyoming. The reason behind this suspension is because of the potential of the seeds to contaminate the wheat crop with human allergens. Therefore, buckwheat can be planted only where commodity wheat is not grown (USDA-NRCS, 2006).

Given the economic damage caused by WSS and the challenges to manage its population, there is a need to invest in better integrated pest management strategies. This can include improvements on conservation biological control strategies because the literature supports the conservation and enhancement of *B. cephi* and *B. lissogaster* as efficient natural enemies in controlling this pest. Therefore, I aim to further investigate the benefits of supplemental nutrition to these braconid parasitoids.

Research Questions

This project is part of the development of an integrated pest management program for wheat stem sawfly that focuses on increasing the number and fitness of the biological control agents *B. cephi* and *B. lissogaster*. Specifically, we are assessing the effects of supplemental nutrition on female parasitoid biology and how it can improve the success of these braconid parasitoids as natural enemies. The primary goals of the research are as follows:

i. To examine *B. cephi* and *B. lissogaster* longevity, egg load, and volume based on carbohydrate-rich diets, whether combined or not with amino acids (Chapter 2).
ii. To evaluate the effects of cowpea extrafloral nectars on *B. cephi* and *B. lissogaster* longevity, egg load, and volume, and assess parasitoid attractiveness to cowpea volatiles (Chapter 3).
iii. To summarize the discoveries from this research and shed light on potential future research (Chapter 4).

As noticed in previous research in our lab, both braconid species increased longevity and egg load when fed sucrose diets, with *B. cephi* also increasing egg volume (Reis et al., 2019). In addition, Reis (2018) observed that some nectars improve these parasitoids egg load, with *B. cephi* also enhancing longevity and egg volume. Here, we hypothesize that *B. cephi* and *B. lissogaster* will display improvements on their longevity, egg load, and egg volume with the nutritional supplementation being offered in our studies. We also expect to see differences in these parameters based on the different species.

In this research we will also conduct surveys of flowering species on remnant prairie in Montana (Appendix A). With this information it will be possible to identify candidate plant species for flower strips or pollinator areas in the Montana wheat-growing region known as the Golden Triangle. In addition, we will conduct an initial assessment of cowpea suitability for Montana field conditions, where we will basally assess growth rates, presence of extrafloral nectars, and yield (Appendix B).

Plant species used as a food supplement in conservation biocontrol programs should benefit growers, natural enemies, and the wildland entomofauna. Therefore, our investigations on the exotic, warm-season cowpea, together with the nutritional requirements and reproductive behavior in *B. cephi* and *B. lissogaster*, is a step forward to improve the conservation biocontrol of wheat stem sawfly across the Northern Great Plains.

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CHAPTER TWO

EFFECTS OF DIETARY SUGARS AND AMINO ACIDS ON LONGEVITY AND REPRODUCTIVE PARAMETERS OF *Bracon cephi* AND *B. lissogaster*, TWO PARASITOIDS THAT SPECIALIZE ON WHEAT STEM SAWFLY

Contribution of Authors and Co-Authors

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Effects of dietary sugars and amino acids on longevity and reproductive parameters of *Bracon cephi* and *B. lissogaster*, two parasitoids that specialize on wheat stem sawfly

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Keywords: egg size; egg load; nutrition; synovigenic; reproductive physiology; *Cephus cinctus;* conservation biological control; integrated pest management

Abstract

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is a major pest of wheat on the Northern Great Plains and Canadian Prairies of North America, causing economic losses of as much as $350 million annually. Two species that parasitize wheat stem sawfly larvae in wheat stems are *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae). Carbohydrate-rich diets increase adult parasitoid longevity and reproductive parameters, enhancing their success as natural enemies. In previous studies, these species had increased longevity, egg load, and volume when fed sucrose solutions, encouraging further research on their nutritional needs. Therefore, we conducted experiments with artificial diets with adult females fed sucrose, glucose, and fructose solutions. Females were also fed these sugars in combination with a mixture of amino acids. We assessed individuals daily for longevity. Both species benefited from diets containing carbohydrates, with an increase in longevity from an average of 9 to 51 days for *B. cephi*, and from 6 to 34 days for *B. lissogaster*. Additional experiments assessed egg load and volume after 2, 5, and 10 days of cumulative feeding in *B. cephi*. These females produced 1.4-fold more eggs when fed amino acids, 2.5-fold more with sugar, and 2.7-fold more when fed sugar with amino acids. They had a 1.3-fold increase in egg volume when fed amino acids, 1.9-fold with sugar, and 2.1-fold when fed sugar with amino acids. Our study reveals nutritional requirements of these braconid parasitoids and the benefits of nutritional sources when implementing conservation biological control strategies.

Introduction

Food sources can play an important role for hymenopteran parasitoids, by increasing their longevity, development, fecundity, and rates of parasitism (Lee et al., 2004; Lee and Heimpel, 2008; Tunçbilek et al., 2012). Plant species that improve parasitoid performance as biological control agents by providing food supplies such as floral and extrafloral nectar are desirable, especially in agricultural systems (Bianchi et al., 2006; Gurr et al., 2017; Heimpel and Jervis, 2005; Simpson et al., 2011; Stephens et al., 1998; Tena et al., 2015). Supplemental nutrition plays a critical role in insect metabolism. However, fundamental knowledge is required on relative use of mono and disaccharides, as well as supplementary amino acids in species that have specific dietary limitations as adults, such as the parasitoids *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae) which do not host feed (Reis et al., 2019). These two biological control agents are well known for suppressing locally damaging populations of wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), which causes severe economic losses in the Northern Great Plains of North America (Bekkerman and Weaver, 2018; Beres et al., 2011; Morrill et al., 1998; Peterson et al., 2011; Weaver et al., 2005). In addition, the availability of supplemental food sources has been shown to benefit both *B. cephi* and *B. lissogaster* (Rand and Waters, 2020; Reis et al., 2019).

The life cycles and biology of *B. cephi* and *B. lissogaster* are similar, with two generations per year (Criddle, 1923; Morrill, 1997; Nelson and Farstad, 1953), where the second generation has a lengthy diapause period during fall and winter (Holmes et al., 1963; Somsen and Luginbill, 1956). The immature parasitoids feed on and kill the wheat stem sawfly larvae, completing their development in approximately 10 days (Nelson and Farstad, 1953; Holmes et al., 1963). After completing the life cycle, *B. cephi* and *B. lissogaster* adults emerge by chewing a hole through the wheat stem, moving to the exterior (Nelson and Farstad, 1953). Both species are specialist ectoparasitoids (Nelson and Farstad, 1953; Somsen and Luginbill, 1956). However, *B. lissogaster* is gregarious and lays as many as four eggs per host (Somsen and Luginbill Jr, 1956), while *B. cephi* is solitary and lays one egg per host (Nelson and Farstad, 1953). Both species are synovigenic, so they do not have a full complement of mature eggs before beginning oviposition (Flanders, 1950). Synovigenic individuals can benefit from nectar availability by increasing longevity and fecundity, thus increasing their success as biological control agents (Jervis et al., 2008; Manandhar and Wright, 2016). This is even more important for those species which are not known to host feed, as is the case for *B. cephi* and *B. lissogaster* (Reis et al., 2019).

Even though parasitoid larvae feed on their arthropod hosts (Balzan and Wäckers, 2013; Godfray, 1994), the majority of adult parasitoids use supplemental carbohydrates, such as floral and extrafloral nectar (Wäckers, 2005), as a primary source of energy (Benelli et al., 2017; Casas et al., 2005; Heimpel and Jervis, 2005; Jervis et al., 2008; Rivero and Casas, 1999; Wäckers, 2005). It is well known that in agricultural systems parasitoids increase their performance as biological control agents when floral and extrafloral nectar are available (Berndt et al., 2006; Bianchi et al., 2006; Gurr et al., 2017; Heimpel and Jervis, 2005; Lee and Heimpel, 2003; Simpson et al., 2011; Stephens et al., 1998; Tena et al., 2015; Tylianakis et al., 2004). Under field conditions, *B. cephi* has been observed foraging on flowers and potentially consuming nectar (Nelson and Farstad, 1953), while under lab conditions, *B. lissogaster* was initially reared with honey and sugar solutions to increase longevity as part of general biological investigations (Somsen and Luginbill Jr, 1956). Reis et al. (2019) reported that a sucrose solution had a positive effect on reproductive success of these braconid parasitoids, in which *B. cephi* and *B. lissogaster* both experience increased longevity and greater egg loads, while egg volume in *B. cephi* also increases when feeding on sucrose. Interestingly, Reis (2018), showed that *B. cephi* increased longevity and both egg load and volume when fed buckwheat nectar and extrafloral nectar, as well as greater longevity with nectar of several other floral species. Rand and Waters (2020) also observed that *B. cephi* has increased longevity when fed buckwheat nectar and coincident aphid honeydew, which are both carbohydrate-rich resources.

Carbohydrates can be used in the process of lipogenesis to synthesize lipids, the main constituent of the fat body in insects (Arrese and Soulages, 2010). The fat body is the tissue involved in key metabolic processes like transamination, and vitellogenin production, forming the proteins that will become yolk protein in eggs (Hoshizaki, 2013). However, some parasitoid species have been shown to be unable to synthesize lipids from excess carbohydrates (Casas et al., 2003; Giron and Casas, 2003; Olson et al., 2000; Rivero and West, 2002; Visser and Ellers, 2008). Other studies with parasitoids have suggested that their performance changes when they feed on different carbohydrates. Luo et al. (2010) noticed that parasitoid females accumulate fructose and total sugars, in addition to having greater longevity and egg reproduction when fed fructose, glucose, and sucrose. Similarly, the non-hymenopteran parasitoid, *Pseudacteon tricuspis* Borgmeier (Diptera: Phoridae), accumulates higher concentrations of sugars and glycogen when fed sucrose, trehalose, glucose, and fructose, with these sugars being related to an increase in their longevity (Chen and Fadamiro, 2006). Therefore, individual mono- or polysaccharides can play different roles in parasitoid physiology. Honeydew with higher concentrations of monosaccharides (glucose and fructose) increases *Aphidius ervi* Haliday (Hymenoptera: Braconidae) longevity when compared to honeydew with higher concentrations of the disaccharide sucrose (Hogervorst et al., 2007), while *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae) has greater longevity when fed the disaccharide sucrose, followed by other monosaccharides (Özalp and Emre, 2001).

To improve biological control of the wheat stem sawfly, it is critical to better understand the benefits of nutritional resources on the reproductive biology of these sympatric parasitoids. Therefore, we further investigate the importance that supplemental food sources might have for *B. cephi* and *B. lissogaster*, which already have been shown to benefit from a supplemental disaccharide. This information will provide better understanding of the dietary needs of these species, as well as other non-host feeding adult parasitoids. In addition, practical adaptation of this knowledge may provide a powerful opportunity to increase parasitoid populations at the field level and allow for implementation of a more resilient biological control program for wheat stem sawfly.

Materials and Methods

We conducted laboratory experiments with adult females of both *B. cephi* and *B. lissogaster* reared on individual monosaccharide or disaccharide solutions in isolation or when combined with amino acids. Newly emerged females were used to quantify the effects of glucose and fructose, with or without supplemental amino acids on female longevity. In addition, we also observed the effects of these diets on *B. cephi* reproductive parameters, where eggs were counted and assayed after feeding for 2, 5, or 10 days.

Parasitoids

Parasitoid cocoons were collected from field samples that were dissected in 2019 and 2020 and stored in plastic bags (16.5 x 14.9 cm) at 0-4°C to prevent development and emergence until use. About three weeks before experiments, parasitoid cocoons were placed in glass jars (236 ml) and maintained in a growth chamber under controlled conditions (25±2°C, 40-60% humidity, and photoperiod LD 12:12 h) for several weeks, until adult parasitoids emerged.

In addition, row samples of wheat stems and stubs were field collected in Montana, USA. In 2019, these were from near Amsterdam, Montana, USA (45° 45’32.4”N, 111° 23’49.2”W) and in 2020 these were again from near Amsterdam (45° 45’32.4”N, 111° 23’49.2”W), and also from near Big Sandy, Montana, USA (48° 10’51.6”N, 110° 20’34.8”W), and near Conrad, Montana, USA (48° 18’11.9”N, 111° 55’22.2”W).

Stems and stubs were placed inside black plastic barrels (121 L, 56x63x71 cm) with lids that had a circular hole (11-cm diameter) in the center, where a clear plastic jar (500 ml; S-22855; Uline, Pleasant Prairie, Wisconsin) was fixed to the top to trap emerging adults. To assist parasitoid movement from the inside of the barrel to the plastic jar, a tapered cone made from clear laminate sheet glued with silicone sealant (GE5000; GE, Boston, Massachusetts) was used. Barrels were kept at room temperature until parasitoid emergence ended. During this interval, the row-sample residue was occasionally misted with water using a hand sprayer to facilitate development and, more importantly, emergence from desiccated stems.

Both jars and barrels were checked daily to collect all overwintering newly emerged adults, with females immediately randomly assigned to the treatments. The number of females available for use in each experiment differed based on variation in population density and species composition for different locations, so the assignment of individuals to treatments followed the approach used by Reis et al. (2019). Adult parasitoid identification was based on several distinguishing morphological characters (Runyon et al., 2001) and any individuals not readily assigned to species were discarded.

Longevity and body size Newly emerged females of *B. cephi* and *B. lissogaster* were fed artificial diets to assess the influence of nutrient components on their longevity. These experiments were conducted in growth chambers (25±2°C, 40-60% humidity, and a LD 12:12 h photoperiod), where individual females were held in plastic petri dishes along with nutrients provisioned via a piece of dental cotton roll soaked in the treatment solutions (Reis et al. 2019). Individuals were randomly assigned to one of eight treatments: sucrose, glucose, fructose in isolation or combined with amino acids, and a water control (Table 2.1), with a total of 30 females per treatment. The diet compositions were chosen because they have been used in several other studies using dietary amino acids (Mevi-Schütz and Erhardt, 2017). The petri dishes were placed inside the growth chamber and the females were inspected daily to record mortality and to provision with new diet-soaked cotton rolls.

After death, as an estimate of parasitoid body size (Jervis et al., 2003), we measured the hind tibiae using a Dino-Lite microscope (model AM7115MZT-Edge, Dino-Lite, Hsinchu, Taiwan) at 50x magnification using the associated computer software (DinoXcope version 1.5.15). These measurements are needed because female size can influence longevity, egg load, and egg volume (Ellers and Jervis, 2003; Jervis et al., 2003; Reis et al., 2019; Saeki and Crowley, 2013).

Egg load and volume – *B. cephi* To assess egg load and volume in *B. cephi*, newly emerged females were fed these same artificial diets, comprising distilled water, amino acids, sugars, or sugars combined with amino acids (Table 1), where 15 females were tested for each treatment.

In previous lab observations, we noticed that females consuming only water die after an average of 10 days, meaning that this is the maximum number of days we conducted experiments to evaluate egg load and volume. Females were randomly assigned to the different treatments and placed in petri dishes under growth chamber conditions. These assays were made after feeding on the diet for 2, 5, and 10 days. Later, female parasitoids were freeze-killed and stored at -30°C until being dissected in distilled water using microdissection forceps to isolate and count eggs under a stereomicroscope (MZ95; Leica, Germany) at 2× magnification. Egg size was measured using a Dino-Lite digital camera (AM7115MZT-Edge, Dino-Lite, AnMo Electronics Corp., Hsinchu, Taiwan) by measuring the length and the diameter at the midpoint of its long axis of each mature egg. Only mature eggs were considered during these experiments (Iwata, 1959). Egg volume (µl) was estimated using the formula $V = (\pi r^2)(L-2r) + (4/3)(\pi r^3)$, where L = length, D = diameter and r = D/2 (O'Neill et al., 2014).

Statistical Analysis

The statistical analyses were conducted using R (R Core Team, 2019) in the integrated development environment RStudio (version 3.6.1). Assumptions were checked by using diagnostic plots generated with the 'car' package (Fox and Weisberg, 2019). Models were simplified through stepwise deletion of terms based on the p-value ($P < 0.05$); interactions that did not meet the criteria were dropped from the model. The effect of artificial diets on longevity was analyzed using the Poisson Generalized Linear Model, where we tested the effects of different experiment years (2019 and 2020) and body size (tibia length). Based on Reis et al. (2019), there is *a priori* expectation that different parasitoid species (*B. cephi* and *B. lissogaster*) will have different longevity responses; therefore, we also tested for a species effect to confirm this. Multiple comparisons were made using Tukey's post-hoc test at $P \leq 0.05$. To test the effects of diet over time on egg load, we followed the procedures as described for longevity. For egg volume, we used linear models and the assumptions of normality and homoscedasticity were met, therefore, transformation of the data was not needed, as was true for the other parameters.

Results

Longevity

Comparing experiments conducted in 2019 and 2020 with both parasitoid species, we measured a strong influence on longevity based on the different treatments ($F_{7, 896} = 285.41$, p <

0.0001) and different species ($F_{1, 896} = 315.90$, $p < 0.0001$), with *B. cephi* living longer than *B. lissogaster* (Fig. 2.1 and Fig. S2.1). In both cases, the water control and amino acid only diets had the lowest longevity. In addition, we detected an influence on longevity based on an interaction of body size and year ($F_{1, 896} = 5.16$, $p < 0.004$), with bigger females living longer in 2019 (Fig. S2.2). There is also an interaction between body size and species ($F_{1, 896} = 4.35$, $p < 0.004$), with *B. cephi* females tending to be bigger (Fig.S2.3). In addition, we found weak evidence for an interaction between treatment and species on longevity ($F_{7, 896} = 1.92$, $p = 0.006$), with both species increasing longevity further with glucose, when compared to other treatments (Fig. 2.1A, B). However, there was a noticeable difference in patterns between *B. cephi* and *B. lissogaster*, with *B. lissogaster* females benefitting further from monosaccharides combined with amino acids (Fig. 2.1A) when compared to *B. cephi* (Fig. 2.1B). In addition, *B. lissogaster* females fed fructose combined with amino acids had slightly increased longevity when compared to either the water control or a fructose solution, but *B. cephi* had the opposite outcome with this diet – a slight decrease in longevity when amino acids were combined with fructose (Fig. S2.1).

Egg Load and Volume – *B. cephi*

There is evidence to support the influence of body size on egg load for *B. cephi* ($F_{1, 173} = 13.14$, $p < 0.004$), with larger females having more eggs (Fig. S2.4). There were also effects of diet ($F_{3, 173} = 31.06$, $p < 0.0001$) and cumulative days of feeding ($F_{2, 173} = 38.13$, $p < 0.0001$) on egg load. Overall, there was an increase in egg load from day 2 to day 5, which was then similar on day 10 (Fig. 2.2, and Fig. S2.5). Our water control had the smallest egg load in isolation, as well as when combined with amino acids, but there was a tendency to increase egg load when water was combined with amino acids, and the same pattern was noticeable when combining sugars with amino acids (Fig. 2.2 and Table S2.1).

There is strong statistical evidence to support the hypothesis that egg volume differs based on the different treatments ($F_{3, 173} = 24.05$, $p < 0.0001$), with our water controls and isolated amino acids solution having the lowest volumes (Fig. 2.3). Our results showed an influence of cumulative days of feeding ($F_{2, 173} = 11.39$, $p < 0.0001$), with egg volume having a significant increase from day 2 to day 5 (Fig. S2.6). We also observed an influence of body size on egg volume ($F_{1, 173} = 13.97$, $p < 0.004$), in which larger females had larger eggs (Fig. S2.7). Even though we did not find strong evidence suggesting an interaction between “treatment” and “day”, we noticed a tendency in *B. cephi* females to increase egg volume when both water and sugars were combined with amino acids (Fig. 2.3 and Table S2.1).

Discussion

Sugar feeding is essential to increase parasitoid reproductive success (Siekmann et al., 2001), and several studies have been shown that supplemental nutrition can benefit longevity, fecundity, and rates of parasitism (Heimpel et al., 1997; Lee and Heimpel, 2008; Lee et al., 2004; Lewis et al., 1998; Tunçbilek et al., 2012). Even though it is not yet well known how adults of *B. cephi* and *B. lissogaster* can benefit from supplemental nutrition, Reis et al. (2019) demonstrated the benefits of dietary sucrose on the adults of these parasitoids. Sucrose increased both *B. cephi* and *B. lissogaster* longevity and egg load, while also increasing egg volume for *B. cephi* (Reis et al. 2019). In our study, we observed that feeding on either monosaccharides or disaccharides was key to increase adult female longevity. We also observed an influence of different carbohydrate molecules on the increases in egg load and egg volume in *B. cephi*. Therefore, supplemental nutrition with saccharides positively affects these female parasitoids, benefiting their metabolism and reproductive biology – with differing effects depending on the molecular structure.

Our results indicate that both species fed on carbohydrates had increased longevity when compared to water and a water solution of amino acids. These braconid parasitoids are able to use provisioned carbohydrates, indicating the influence of the digestive enzyme α-glucosidase, which is involved in hydrolyses of certain saccharides (Chippendale, 1978), which are, in turn, key in the successful use of these energy sources. Our observations corroborate results observed for these species when fed sucrose (Reis et al., 2019), and other studies have indicated that carbohydrate-rich diets can increase longevity and fecundity in parasitic hymenopterans (Heimpel et al., 1997; Lewis et al., 1998). In addition, Xiong et al. (2020) observed a correlation between longevity and the expression of certain lifespan-related genes when comparing wasps fed different concentrations of sucrose and honey, suggesting that not only the concentrations, but also the type of saccharide molecule can change genes expression and how these determine insect longevity.

When comparing the monosaccharide sugars tested in our research, there was a tendency for glucose to better benefit longevity when compared to the monosaccharide fructose or the disaccharide sucrose, which is combined glucose and fructose. This is an interesting result because insect hemolymph contains mostly trehalose (which is two molecules of glucose combined together), and is synthesized in the fat body as an important carbohydrate reserve (Arrese and Soulages, 2010; Rivero and Casas, 1999). As the amount of trehalose increases to a critical concentration in the hemolymph, synthesis is interrupted and glycogen synthesis takes place instead (Arrese and Soulages, 2010). Chen and Fadamiro (2006) reported that age plays an important role in glycogen levels, with the levels decreasing in older individuals. In addition to age, the diets also influenced glycogen content, with sugars helping to maintain glycogen levels (Chen and Fadamiro, 2006; Luo et al., 2010). The parasitoid *Diglyphus isaea* Walker (Hymenoptera: Eulophidae) was able to use sucrose and convert it to glycogen and body sugars, but it could not convert it into lipids (Zhang et al., 2011). Many parasitoid species are not able to synthesize lipids from carbohydrates (Akman Gündüz et al., 2010; Olson et al., 2000; Rivero and West, 2002; Zhang et al., 2011), and parasitoids emerge with a considerable reserve of lipids that decrease with age (Akman Gündüz et al., 2010).

Dietary fructose can be combined with other molecules such as biphosphate, and act on the regulation of glycolysis (Arrese and Soulages, 2010). Knowing that insects absorb carbohydrates in their guts as monosaccharide sugars, and that all insects can use metabolic intermediates from lipid and amino acids to synthesize glucose by gluconeogenesis (Douglas and Simpson, 2013), we hypothesize that females feeding on glucose can rapidly use this sugar or have it easily combined to yield trehalose, avoiding or decreasing the gluconeogenesis process. As a consequence, they may be conserving energy and preserving metabolic resources that might be crucial for other physiological processes, perhaps increasing their longevity.

Other diet compounds in addition to carbohydrates can be important for the survival and reproductive success of insects (Levin et al., 2017). Another objective of our study was to determine if amino acids could further increase *B. cephi* and *B. lissogaster* longevity, as has been found for certain other nectar-feeding species (Berndt and Wratten, 2005; Tompkins et al., 2010). Our results show that females fed on water combined with amino acids did not have increased longevity, confirming that carbohydrates are critical in maintaining homeostasis and optimal metabolism. In addition, carbohydrates combined with amino acids did not benefit female longevity. Insects can convert carbohydrates into certain proteins, but the opposite is not true. Even though this process is costly, and the rate of occurrence is limited (Hoshizaki, 2013), females could be benefitting by this process when fed carbohydrates, but not when amino acids were present in the diet. In addition, the food intake by hymenopteran parasitoids is limited by their stomach volume and not caloric consumption (Ellers et al., 2011), therefore, the parasitoids used in our study might need to feed on a broader range of nutrient concentrations to show a significant increase in longevity when comparing diets containing sugars with amino acids. Our results for longevity could also indicate an allocation of these amino acids to the reproductive system, as observed in studies with lepidopterans (Levin et al., 2017; Mevi-Schütz and Erhardt, 2017), or vitellogenin synthesis and fecundity in the crop pest *Nilaparvata lugens* (Stål) (Lu et al., 2016). Perhaps consequently, we do not see an increase in longevity when carbohydrates are combined with amino acids.

To better clarify and investigate how carbohydrates and amino acids benefit female parasitoids, we analyzed egg load and volume with *B. cephi* females fed for 2, 5, and 10 days on artificial diets. These different diets contained water, amino acids only, sugars (fructose, sucrose, and glucose), or sugars combined with amino acids. Our results showed that there is an influence of sugars and sugars combined with amino acids on egg load and volume. Levin et al. (2017)

noticed that adult moths allocate amino acids to flight muscles and eggs, which are also detectable in their offspring (1st and 2nd instars), showing that dietary amino acids are essential in the quality of eggs and young offspring (Levin et al., 2017). Although the Levin et al. (2017) experiments were conducted with Lepidoptera, it is possible that our braconid female parasitoids are also allocating similar nutrient resources to their eggs to improve offspring quality and fitness. This could be an important strategy being used by our synovigenic parasitoids, especially because the adults are not known to host feed on *C. cinctus* (Reis et al., 2019), which could otherwise be a dietary source of amino acids.

We also noticed a tendency for amino acids combined with sugars to significantly increase egg load and volume in earlier stages (when comparing specific results from day 2 to both day 5 and 10). On day 2, there was an increase in both egg load and volume, reaching 67% and 46% greater, respectively. In addition, when carbohydrates were not present, amino acids seemed to boost these parameters when compared to our control, especially on day 2, with an increase of 62% in egg load and 76% in egg volume. This suggests that these female parasitoids are using nutrients for metabolism as well as to improve their reproductive reserves. Females used in our experiments were 1st generation, and thus, they might be benefitting from a nutrient restoration after overwintering (Nelson and Farstad, 1953). In addition, females might be incorporating some of these nutrients in their eggs (Levin et al. 2017). Amino acids are important for oocyte growth, yolk development, and ovulation and oviposition (Hegdekar, 1970), but logistical challenges in our system prevented us from experimental study of oviposition.

Therefore, amino acid nutrition could be additionally benefiting these female parasitoids, although this lay outside the scope of our study.

Some of the amino acids used in our study are important to insects, such as glutamate that plays a central role in transamination reactions (Douglas and Simpson, 2013), or tyrosine that is used for cuticle sclerotization and is also a constituent of some proteins (Hoshizaki, 2013). Proline is an energy source used for flight (Douglas and Simpson, 2013), but in our study we did not analyze the flight performance of female parasitoids, and thus it is unknown if diets could be influencing parasitoid flight directly or indirectly via increased longevity. In addition, amino acids from insect diets can interact with symbiotic microorganisms, influencing their ability to control bacterial growth (Chandler et al., 2008; Lee et al., 2006), and viral pathogens (Lee et al., 2006). Host diet can also be an important nutritional source for the maintenance of symbionts to provide other nutrients, and symbionts may be critical to the host wheat stem sawfly larvae (Yeoman et al., 2019). Even though parasitoids can benefit from products derived from host symbionts, there is no evidence to date showing that symbionts in parasitoids provide nutrients to their hosts (Dicke et al., 2020) and there is no information to date on potential *B. cephi* and *B. lissogaster* symbionts. Such knowledge might allow for manipulation of symbioses to affect parasitoid fitness and increase their success as biological control agents. We also acknowledge that we tested lower ratios of carbohydrate to amino acids than those reported by Lee et al. (2015) for another insect species. Therefore, the braconid parasitoids in our experiments may have required a different ratio of carbohydrates to amino acids than was tested to display dietary benefits.

In conclusion, our research aimed to investigate the effects of carbohydrate-rich diets both in combination with amino acids and alone for both *B. cephi* and *B. lissogaster*, two synovigenic specialist ectoparasitoids. Both species benefited from glucose, especially when combined with amino acids. Although there are many similarities between these two species, their longevity follows different patterns, with *B. lissogaster* tending to increase longevity when fed on monosaccharides combined with amino acids. The number of females available for use in each experiment depends on population density and species composition for different locations, so we were not able to analyze egg load and volume for *B. lissogaster*. For *B. cephi* we noticed a strong influence of carbohydrates on egg load and volume, especially during the initial 5 days of adult life, with the addition of amino acids tending to further increase these reproductive parameters. By exploring these parasitoids' specific nutritional requirements and behavior, it is possible to envision a more successful biological control program for wheat stem sawfly. Nevertheless, we encourage more studies to further investigate flight performance, egg composition, and fertility for these parasitoids. In addition, there is a need to explore how other more complex nutritional sources, such as floral and extrafloral nectar and their compositions, could affect these parasitoids. It would then be possible to better understand their nutritional needs and how they benefit the performance of these species as natural enemies of a key agricultural pest.

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Figures

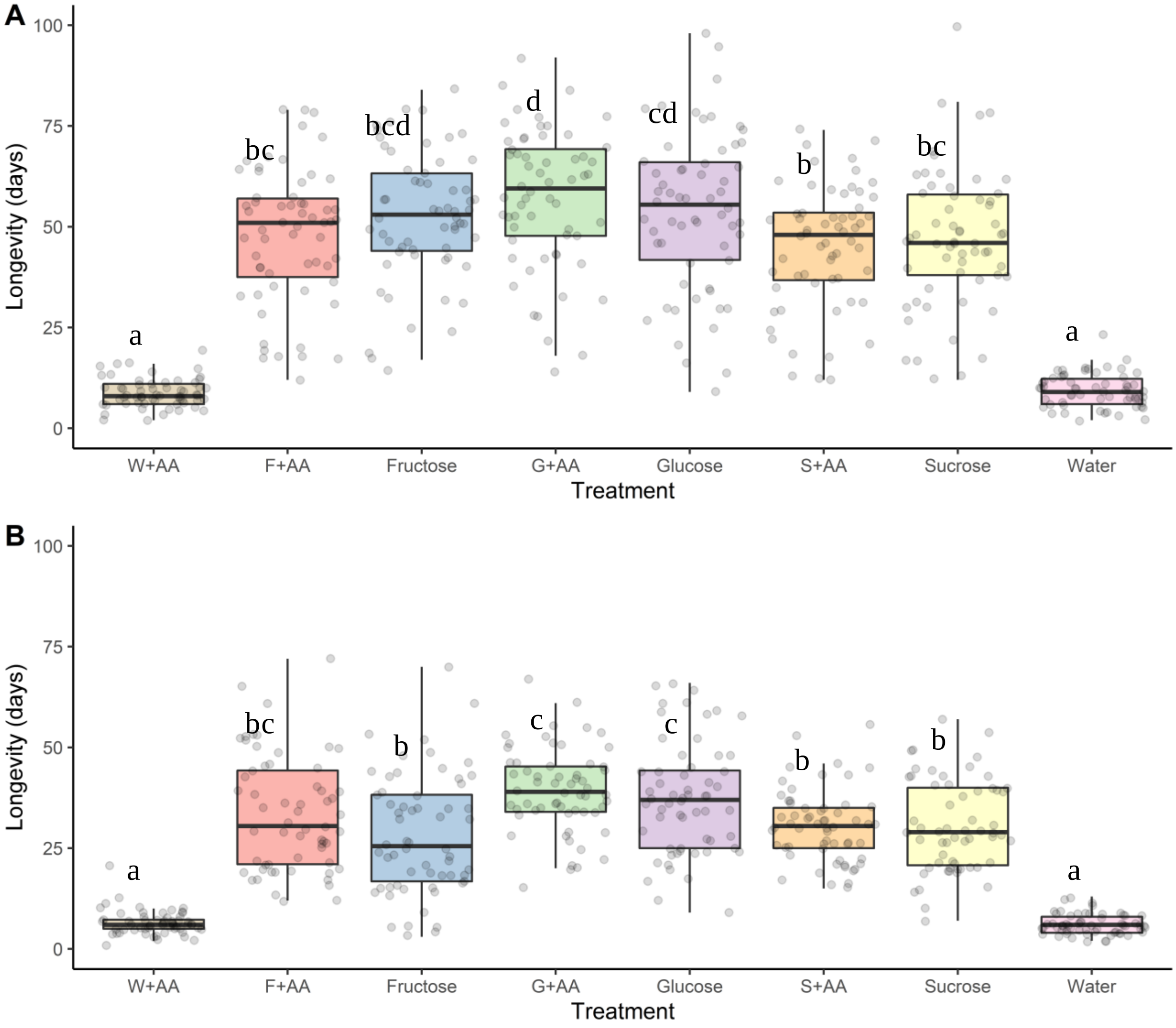

Fig. 2. 1. Mean longevity in number of days of (A) *Bracon cephi* and (B) *B. lissogaster*. Females were fed until death with either water (control), amino acids (W+AA), fructose, sucrose, glucose, or the respective sugars combined with amino acids: fructose plus amino acids (F+AA), sucrose plus amino acids (S+AA), or glucose plus amino acids (G+AA). Groups with the same letter are not different by the pairwise comparison tests, with 5% familywise significance level.

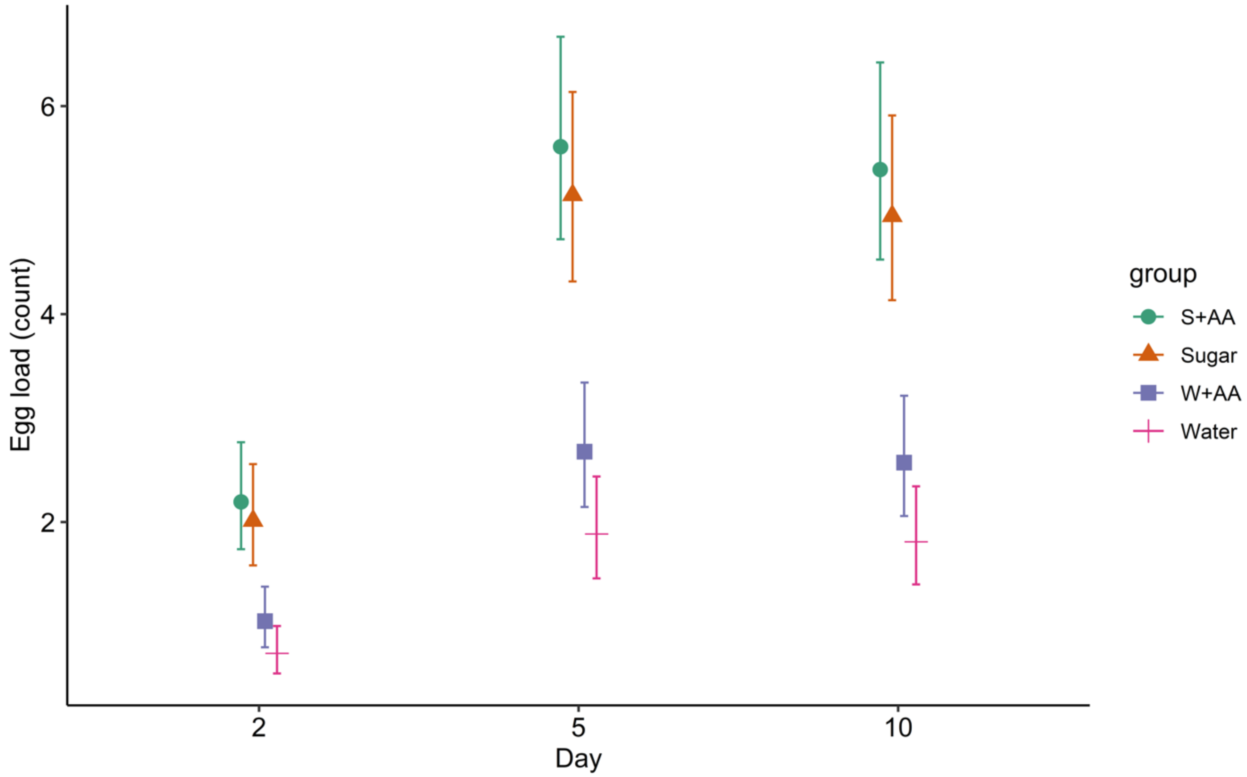

Fig. 2. 2. Predicted values for the mean egg load of *Bracon cephi* with the interaction between cumulative days of feeding and treatments. Diets were offered ad libitum over 2, 5, and 10 days and consisted of either water, water + amino acids (W+AA), sugar, or sugar + amino acids (S+AA).

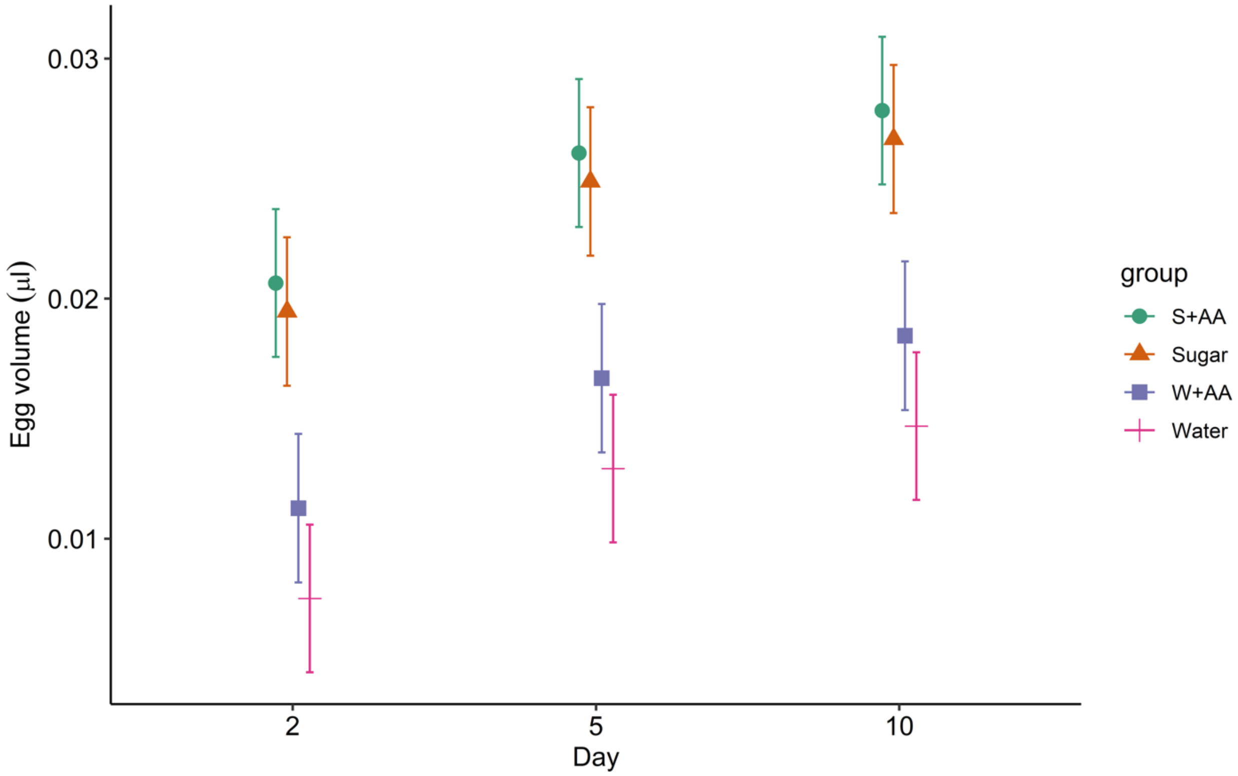

Fig. 2. 3. Predicted values for mean egg volume (µl) of *Bracon cephi* and the interaction of cumulative days of feeding and treatments. Treatments consisted of either water, water + amino acids (W+AA), sugar, or sugar + amino acids (S+AA). Diets were offered ad libitum over 2, 5, and 10 days.

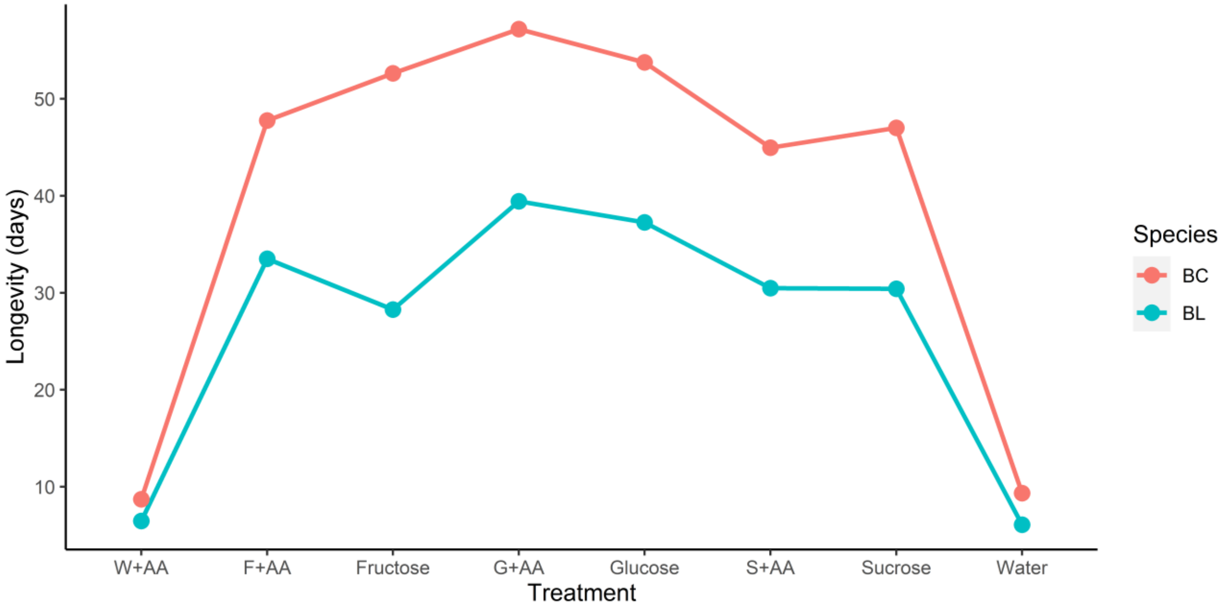

Fig. S2. 1. Mean longevity for (A) *Bracon cephi* (BC) and (B) *B. lissogaster* (BL) on the treatment diets: water (control), amino acids (W+AA), fructose, sucrose, glucose, or the respective sugars combined with amino acids: fructose plus amino acids (F+AA), sucrose plus amino acids (S+AA), or glucose plus amino acids (G+AA).

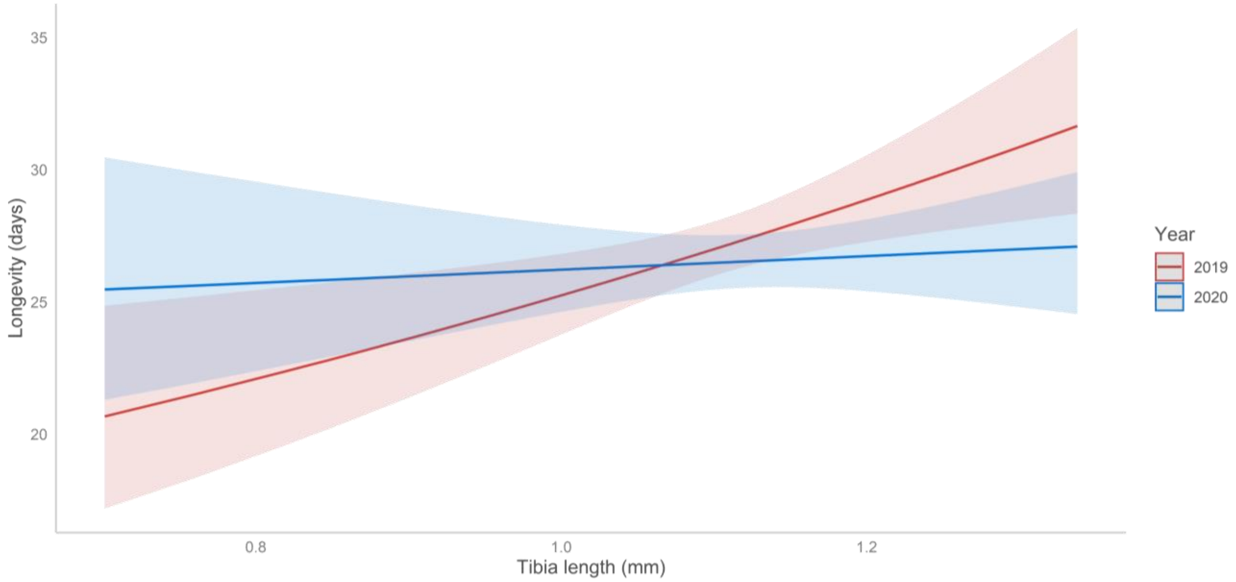

Fig. S2. 2. Effect display of the interaction between experimental years (2019 and 2020) and body size (tibia length in mm) for both *Bracon cephi* and *B. lissogaster*, based on a logit model fit for longevity (days).

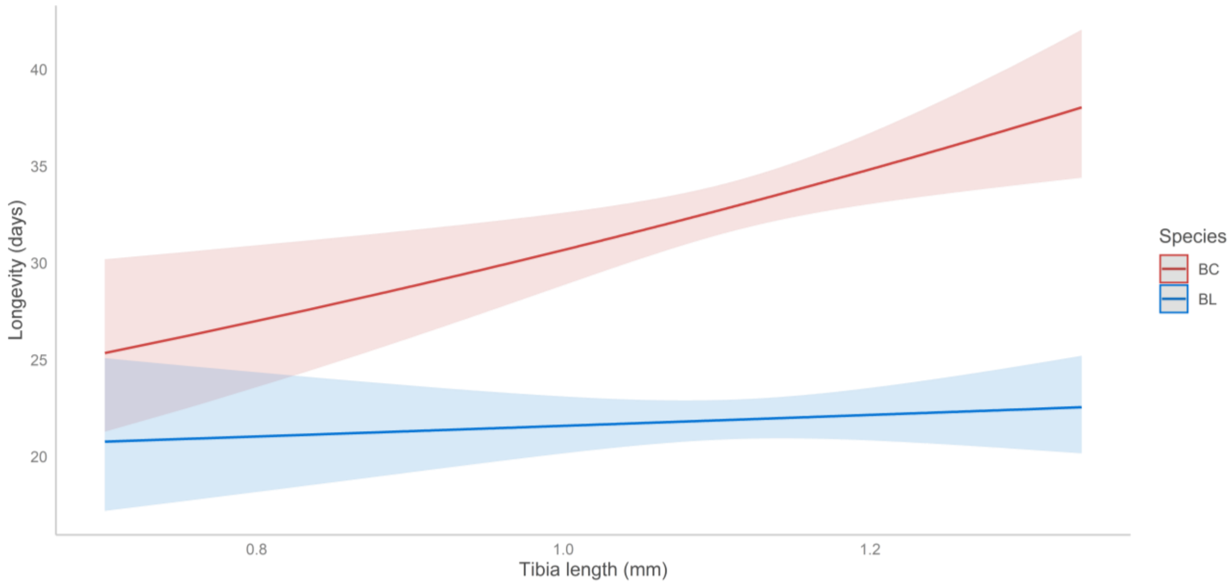

Fig. S2. 3. Effect plot displaying the interactions between the parasitoid species *Bracon cephi* (BC) and *B. lissogaster* (BL) and body size (tibia length in mm), based on a logit model fit for longevity (days).

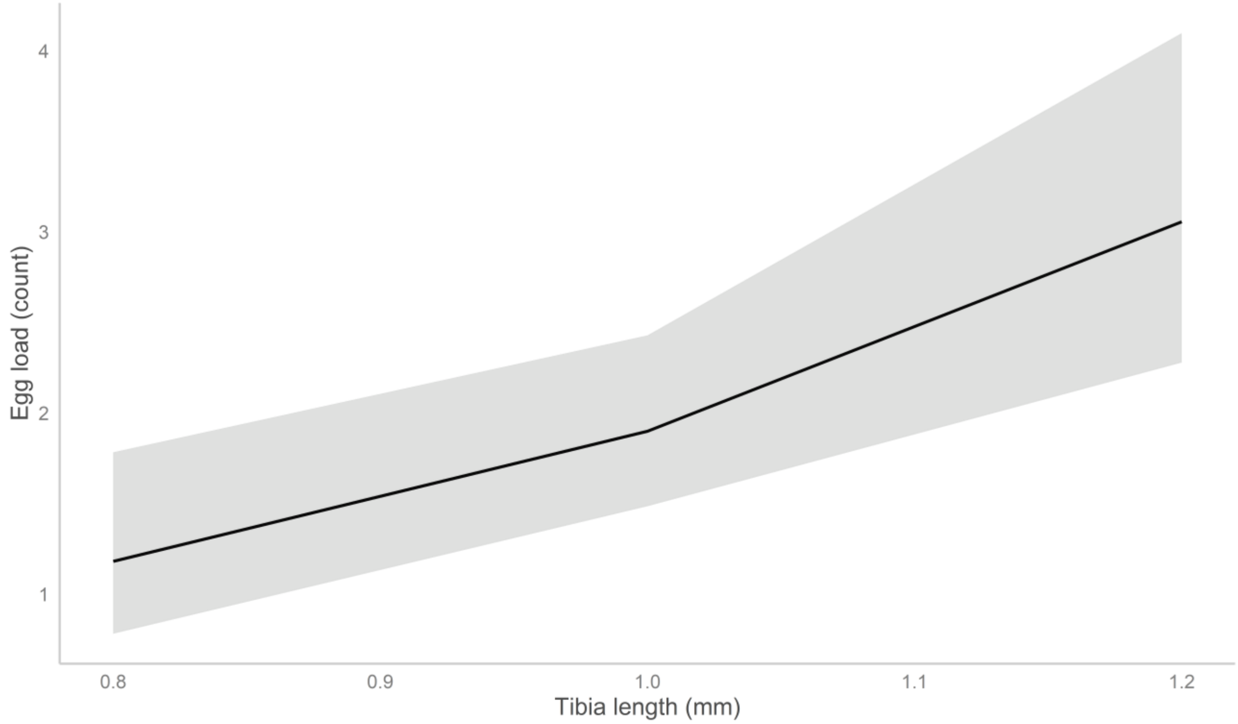

Fig. S2. 4. Relationship between predicted values of mean egg load and body size (tibia length in mm) for *Bracon cephi*.

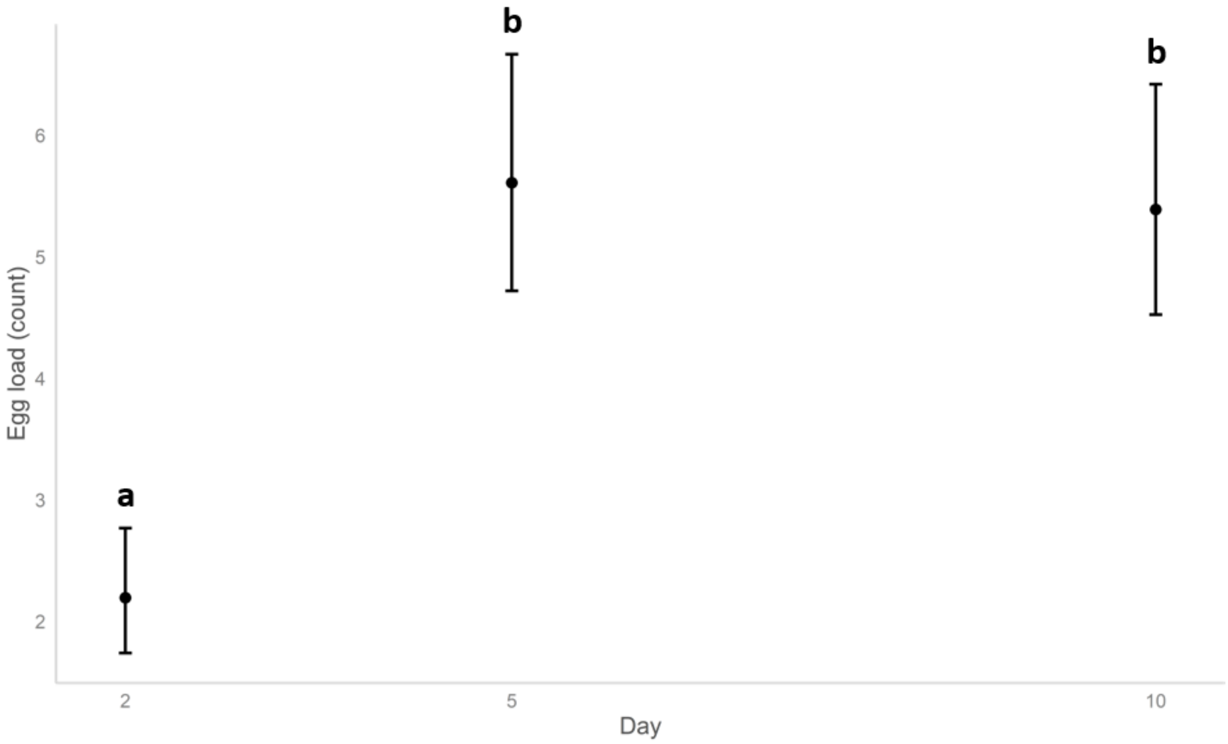

Fig. S2. 5. Predicted values of mean egg load for *Bracon cephi* females for the three days where cumulative feeding effects were measured. Groups with same letter are not different in pairwise comparison tests, with a 5% familywise significance level.

Fig. S2. 6. Predicted values of mean estimated egg volume (µl) for *Bracon cephi* females for the three days where cumulative feeding effects were measured (2, 5, and 10 days). Groups with same letter are not different in pairwise comparison tests, with a 5% familywise significance level.

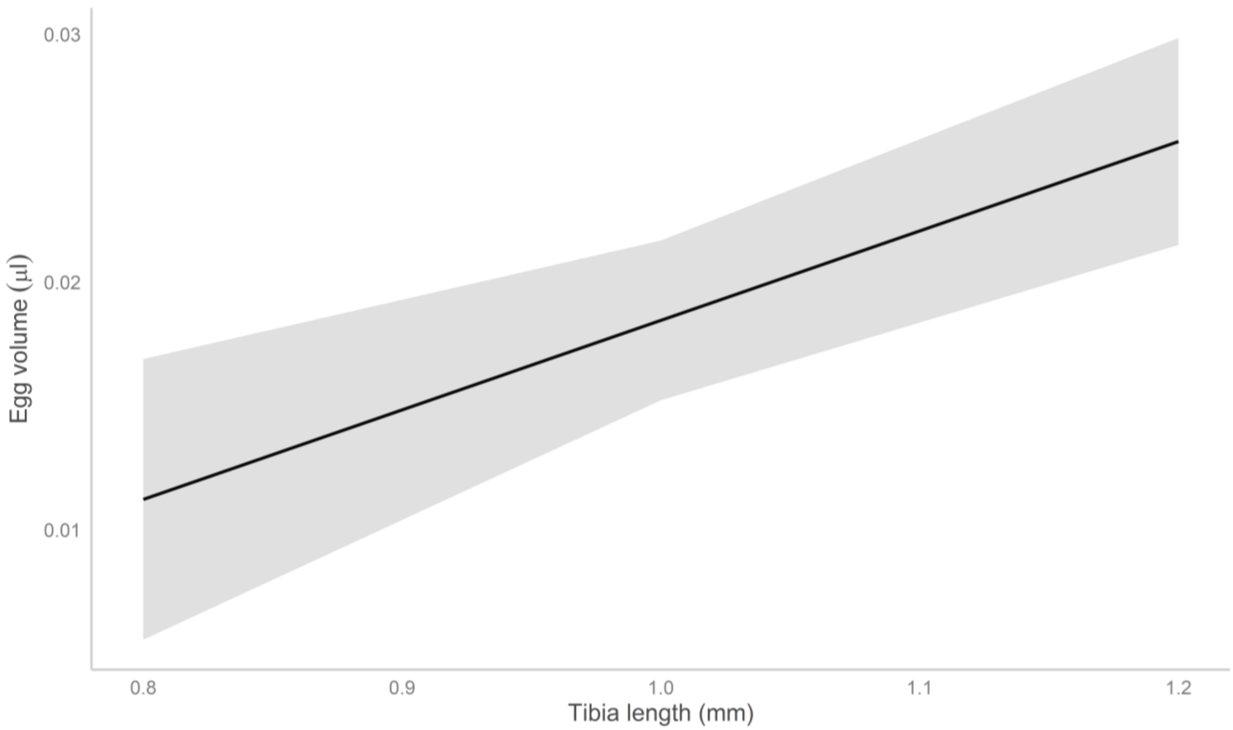

Fig. S2. 7. Relationship between the predicted values of *Bracon cephi* egg volume (μl) and body size (tibia length in mm).

Tables

Table 2.1. Composition of artificial diets used during experiments with *Bracon cephi* and *B. lissogaster*. Sugar concentrations are represented in molar (M) and amino acids in millimolar (mM) units.

Treatment	Components	Concentration
Sugar	sucrose	0.5 M
	fructose	0.5 M
	glucose	0.5 M
Amino Acids	**Essentials**	
	arginine	0.20 mM
	threonine	0.65 mM
	tyrosine	0.20 mM
	valine	0.15 mM
	Non-essentials	
	alanine	0.70 mM
	asparagine	0.40 mM
	glutamic acid	0.35 mM
	glutamine	0.95 mM
	glycine	2.35 mM
	proline	2.25 mM
	serine	1.35 mM

Table S2. 1. Results of calculations for the percentage increases in both egg load and volume for *Bracon cephi* measured after feeding on artificial diet for 2, 5, and 10 days. Artificial diets consisted of water, water combined with amino acids (W+AA), sugars, and sugars combined with amino acids (S+AA). In all cases, percentage increases are for the inclusion of amino acids relative to water or aqueous solutions of sugars.

Egg load			
		Day	
	2	**5**	**10**
W+AA vs Water	62	34	36
S+AA vs Sugar	67	0	1
Egg volume			
		Day	
	2	**5**	**10**
W+AA vs Water	76	26	17
S+AA vs Sugar	46	-3	-4

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CHAPTER THREE

CAN A NON-NATIVE COVER CROP SUPPORT NATIVE PARASITOIDS? COWPEA EXTRAFLORAL NECTAR HAS POTENTIAL TO PROVIDE ECOSSYSTEM SERVICE RESOURCES LOST IN AGRICULTURAL INTENSIFICATION

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Conceived the project; revised, read, and approved the final manuscript

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Contributions: Conceived the project; assisted with data analysis; revised, read, and approved the final manuscript.

Manuscript Information

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Abstract

The native parasitoids *Bracon cephi* and *B. lissogaster* reduce populations of *Cephus cinctus*, an endemic grassland species that has adapted to become a major pest of wheat on the Northern Great Plains. Non-host feeding adults of these braconids increase longevity, egg load, and egg volume when provisioned carbohydrate-rich diets. Nutrition from nectar can enhance their success as natural enemies, while plant species intended for sustainable habitat management should benefit growers by also providing ecosystem services. Cover crop cowpea adds resilient features to the landscape and has extrafloral nectaries (EFN), easy-access nectar sources for beneficial insects. If more cowpea was grown on the Northern Great Plains, will *B. cephi* and *B. lissogaster* benefit from foraging toward non-native cowpea plants to encounter putatively beneficial EFN? We investigated cowpea inflorescence stalk extrafloral nectar (IS-EFN) and leaf stipel extrafloral nectar (LS-EFN) as potential food sources for these parasitoids. Females were caged on EFN sources on living cowpea plants to assess longevity, with a water control. Egg load and volume were measured at 2, 5, and 10 days after placement. *B. cephi* survived 10 days on water, 38 days on IS-EFN; *B. lissogaster* 6 days on water, 28 days on IS-EFN. *B. lissogaster* maintained constant egg load and volume across treatments while *B. cephi* produced 2.1-fold more eggs that were 1.6-fold larger on IS-EFN. Y-tube olfactometry indicates adult female parasitoids were attracted to cowpea volatiles. These results demonstrate that non-native, warm-season cowpea benefits these native parasitoids and may improve conservation biological control of *C. cinctus*.

Introduction

Agricultural systems that provide floral and extrafloral nectar are well known to benefit parasitoids in their role as biological control agents (Bianchi et al., 2006; Gurr et al., 2017; Heimpel and Jervis, 2005; Simpson et al., 2011; Stephens et al., 1998; Tena et al., 2015). Specifically, nectar increases both abundance and the resulting level of parasitism due to these organisms, helping to manage pest populations (Berndt et al., 2006; Lavandero et al., 2005; Tylianakis and Binzer, 2014). Severe economic losses are caused on the Northern Great Plains of North America by wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), a native species (Lesieur et al., 2016) that is a major pest of wheat (Beres et al., 2011a). Two well-known biological control agents can locally suppress wheat stem sawfly populations across the landscape, *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae) (Bekkerman and Weaver, 2018; Beres et al., 2011b; Morrill et al., 1998; Peterson et al., 2011; Weaver et al., 2005). The life history of these native specialist parasitoids may have included access of food resources that could benefit the adult stage on the diverse prairie landscape that existed prior to the planting of wheat and rapid agricultural intensification that began on this landscape in the late 1800s (Adhikari et al., 2018; 2019). This large scale cropping also resulted in new host plant use and a change of common name to reflect the pest status for the previously named western grass-stem sawfly, *C. cinctus* (Ainslie, 1920).

Supplemental Nutrition in *B. cephi* and *B. lissogaster*

B. cephi and B. *lissogaster* are not known to host-feed as adults (Reis et al., 2019) and early reports describe adult nutrient consumption in both species. Adult *B. cephi* fed on floral nectar and water droplets while foraging near headlands and roadsides (Nelson and Farstad, 1953), while initial laboratory studies on the newly described *B. lissogaster* (Muesebeck, 1953) used individuals reared with access to sugar solutions and honey to increase longevity for biological characterization (Somsen and Luginbill, 1956). More recent studies showed that *Bracon cephi* and *B. lissogaster* increased longevity and egg load when fed sucrose solutions, while *B. cephi* also increased egg volume (Reis et al. 2019). Subsequent studies in our lab showed that both species increased longevity when feeding on sugar solutions containing fructose, sucrose, or glucose (Cavallini et al., 2022 – submitted), while *B. cephi* increased egg load and egg volume, with the addition of amino acids tending to further increase these reproductive parameters (Cavallini et al., 2022 – submitted).

Both *B. cephi* and *B. lissogaster* females differed in their longevity, egg load, and egg volume after nectar feeding on certain plant species. *B. cephi* females increased their longevity when provided buckwheat, *Fagopyrum esculentum* Moench, (Rand and Waters, 2020; Reis, 2018) or safflower (*Carthamus tinctorium* L.) nectar (Reis, 2018), and increased egg load and egg volume when provided buckwheat nectar and nectar of deerhorn clarkia (*Clarkia pulchella* Pursh), a native species (Reis, 2018). *B. lissogaster* had increased egg load when provided deerhorn clarkia nectar but did not increase longevity or egg volume when provided deerhorn clarkia, safflower, or buckwheat nectar (Reis, 2018). Buckwheat nectar incrementally increased wheat stem sawfly longevity without increasing egg deposition, and thus it is unlikely to increase population size in this pest (Rand et al., 2019). Regrettably, contamination of wheat grain with seeds from inadvertent harvest of volunteer buckwheat plants poses a risk of human dietary exposure to allergens (Norbäck and Wieslander, 2021; Stember, 2006). Therefore, the USDA Natural Resources and Conservation Service permanently suspended the use of buckwheat in rotation with or adjacent to commodity wheat production in Colorado, Kansas, Idaho, Minnesota, Montana, Nebraska, North Dakota, Oregon, South Dakota, Washington, and Wyoming (USDA-NRCS, 2006), which resulted in the loss of a major potential contributor to ecosystem services in the area under the suspension.

Farming Practices and Natural Enemies

Plant biodiversity supports beneficial insects in agroecosystems by providing them with food resources, pollen, additional shelter, protection, and alternative prey (Adhikari et al., 2018; Gurr et al., 2017; Landis et al., 2000; Perović et al., 2018). However, agricultural intensification, such as landscape simplification and less diverse crop rotations, decrease biodiversity in agroecosystems (Adhikari et al., 2019; Benton et al., 2003; Concepción et al., 2008; Emmerson et al., 2016) In semiarid regions, such as the U.S. Northern Great Plains, dryland farming practices dominate the landscape, and since the 1930s the rotation of cereals with summer fallow has been the principal type of cropping (Stewart and Thapa, 2016). Recently, increasing numbers of farmers use pulse crops in their dryland rotations to replace the fallow component in this wheat-fallow cropping system (Long et al., 2014a, 2014b; Miller et al., 2006). Both pulses and cover crops suppress weeds (Mhlanga et al., 2016; Weisberger et al., 2019), protect and enrich the soil (Crews and Peoples, 2005), and reduce pest pressure while increasing yields in agroecosystems (Bullock, 1992; Kirkegaard et al., 2008; Miller et al., 2002). Replacement of fallow with cover crops affects wheat yield based on the climate of the Northern Great Plains (Carr et al., 2021), with soil water and nitrogen use by the cover crop influencing following wheat productivity (Jones et al., 2020; Miller et al., 2018). Cover crops and pulses also offer nectar that can increase both the efficacy and population sizes of a variety of natural enemies (Heimpel and Jervis, 2005). In Montana, the presence of pulse or cover crops adjacent to wheat often caused small increases in the abundance of the parasitoids *B. cephi* and *B. lissogaster*, which is associated with small decreases in stem lodging caused by wheat stem sawfly larval stem cutting (Fischer, 2019). In addition, cover crops seem to be somewhat more effective than pulse crops in increasing the success of braconid parasitoids in suppressing wheat stem sawfly populations (Fischer, 2019).

Cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae: Papilionoideae), an herbaceous annual plant, is an excellent alternative crop that prevents soil erosion, suppresses weed growth, and provides nitrogen to subsequent crops (Clark, 2012). It is a heat-adapted annual legume (Abate et al., 2011), therefore, is sensitive to freezing temperatures and must be sown after the risk of frost is over.

Cowpea nectar has a high concentration of sugars which can meet nutritional needs of beneficial insect species (Fohouo et al., 2009), and provides nectar to honey bees that visit its inflorescences (Vaz et al., 1998). Cowpea also possesses two types of extrafloral nectaries (EFN), one at the inflorescence stalk (IS-EFN) and another at the stipels of trifoliate leaves (LS-EFN) (Kuo and Pate, 1985; Pate et al., 1985). EFN are an important nectar source for parasitoids and pollinators due to high sugar and amino acid concentrations (Pate et al., 1985), and also readily allow nectar access by smaller species like parasitoids (Patt et al., 1999; Vattala et al., 2006; Wäckers et al., 1996).

A better understanding of the positive effects of cover crops in agroecosystems and the benefits that associated nutrition can provide to parasitoids is important to improved conservation biocontrol in intensified monocultures. Hence, we aimed to characterize the contribution of diverse cowpea EFN on longevity, egg load, and egg volume of braconid parasitoids. In addition, cowpea is an exotic, pantropical species and there are no native species of *Vigna* on the Northern Great Plains. Therefore, there is a need to assess if the native parasitoids, *B. cephi* and *B. lissogaster*, will be attracted to cowpea, as well as forage and consume the two types of EFN it produces. Our findings will help support future careful consideration of benefits of nectar type, specific cover crop and particular ecosystem services aided. These are broad considerations that are applicable worldwide for areas of agricultural intensification, particularly where large cereal crop monocultures may have greatly depleted ecosystem services due to dramatic losses of flowering species on the landscape.

Materials and Methods

Plant Culture

Four cultivars of cowpea, *V. unguiculata*, including two commercial lines (“Victor” and “Chinese red”), and two non-commercial landraces (“PI 527281” and “PI 358716”), and buckwheat (*Fagopyrum esculentum*) were grown under greenhouse conditions at the Montana State University Plant Growth Center in Bozeman, Montana, USA. Seed for the cowpea commercial varieties was donated by Kamprath Seed, Inc. (Manteca, California, USA), and cowpea seeds for the non-commercial landraces were selected from germplasm maintained by USDA, ARS, PGRCU (Griffin, Georgia, USA). The non-commercial lines were chosen based on a consideration of Montana's landscape and climate, in particular to better match climate by greater elevation and with focus toward relatively limited precipitation. "PI 358716" is from Gedo, Ethiopia, at 2500 m in elevation and an average of 91 mm annual precipitation, while "PI 527281" is from Filabusi, Zimbabwe, at 1080 m in elevation and an average of 58 mm precipitation annually.

We sterilized seeds in 55% bleach and rinsed once with distilled water. Later they were germinated in germination boxes and posteriorly sown on pots containing a 50:50 mix of two soils: PGC Soil Mix and Sunshine Mix#1. The PGC Soil Mix consists of equal parts of Bozeman Silt Loam Soil, Washed Concrete Sand, and Canadian Sphagnum Peat Moss. AquaGro 2000 G wetting agent is incorporated at 0.59 kg/m^3 of the soil mix. Sunshine Mix#1 contains Canadian Sphagnum Peat Moss, perlite, vermiculite, starter nutrient charge, wetting agent, and Dolomitic lime, with 5.5-6 pH.

Plants were maintained under greenhouse condition (22℃ ± 2℃ during the day and 20℃ ± 2℃ during the night), with natural and artificial light (photoperiod of 15L:9D h, GE Multivapor lamps model MVR1000/C/U, GE Lighting, General Electric Co., Cleveland, Ohio, USA). We watered plants as needed and fertilized once per week with Peters Professional® General Purpose Fertilizer (J.R. Peters, Inc., Allentown, Pennsylvania, USA) at 100 ppm in aqueous solution. We divided the greenhouse bench in 4 different blocks to account for confounding factors based on their position at the greenhouse.

Parasitoids

The number of females used in each experiment differed based on variation in population density at different sites. Adult parasitoids were collected from wheat stubble samples taken from the field during spring 2020 and spring 2021 as described in Cavallini et al. (Submitted). Briefly, wheat stems and stubs were collected near Amsterdam, Montana, USA (45° 45’32.4”N, 111° 23’49.2”W), near Big Sandy, Montana, USA (48° 10’51.6”N, 110° 20’34.8”W), and near Conrad, Montana, USA (48° 18’11.9”N, 111° 55’22.2”W). We placed the plant material inside black plastic barrels (121L, 56x63x71 cm) with lids containing a circular hole (11 cm diameter) in the center, where a clear plastic jar (500 ml; S-22855; Uline, Pleasant Prairie, Wisconsin) was used to trap emerging adults (Meers, 2005). We kept the barrels in cold storage (7°C ± 2°C, 30-40% humidity) to prevent parasitoid development and adult emergence until they were brought to room temperature. Barrels were then checked daily to collect both *B. cephi* and *B. lissogaster* adult females. Parasitoid identification was made based on morphological characters (Runyon et al., 2001).

Longevity, body size, egg load, and egg volume Newly emerged female parasitoids were collected and held individually in plastic petri dishes containing a dental cotton roll soaked in distilled water for 12–24 h. These naïve parasitoids were used to conduct experiments with cowpea extrafloral nectaries with the cowpea cultivars: “Victor”, “Chinese red”, “PI 358716”, and “PI 527281”. Individuals were randomly assigned among the different treatments: cowpea inflorescence-stalk extrafloral nectar (IS-EFN); cowpea leaf stipel extrafloral nectar (LS-EFN); buckwheat nectar (positive control), or water (negative control). Buckwheat was chosen as a positive control because it is one of the most studied plants in efforts to improve conservation biological control, it is abundant and the nectar is easily accessed (Fiedler et al., 2008), and it is known to benefit both *B. cephi* (Rand and Waters, 2020; Reis, 2018) and *B. lissogaster* females (Reis, 2018).

Females were placed individually in cages made of plastic cocktail cups (226 ml) (Reis et al. (2019). The bottom portion of the cup was removed and covered with tulle fabric (0.3-mm mesh), while in the upper part of the cup a piece of tulle fabric was glued and used to close the cage, preventing females from escaping. Each cage was placed surrounding the respective nectary (IS-EFN, LS-EFN, or buckwheat inflorescence), while water controls were left empty. To hold the cages in place, they were tied to a bamboo stake using a rubber band (size #64). The bamboo stakes were placed on the pot soil near the plant and all cages had water provided on a cotton pad placed on the top of the cup. Females were observed daily to record mortality, re-wet cotton pads, and if necessary, change the cage to a more active nectary.

The total number of *B. cephi* used for this assay was 15 individuals for each treatment (cowpea IS-EFN and LS-EFN; buckwheat nectar, and water). The number of *B. lissogaster* females used for this assay was 12 individuals for each treatment, except for “PI 358716” and “PI 527281” LS-EFN that had 11 and 10 individuals, respectively. To estimate parasitoid body size, we measured the hind tibia (Jervis et al., 2003) because it can be related to the female longevity, egg load, and egg volume (Ellers and Jervis, 2003; Saeki and Crowley, 2013). Hind tibiae were measured using a Dino-Lite microscope (model AM7115MZT-Edge, Dino-Lite, Hsinchu, Taiwan) at 50x magnification and the associated computer software (DinoXcope version 1.5.15).

Egg load and volume were determined using the methods of Reis et al. (2019). Briefly, females were randomly assigned to the different treatments and placed in the cages made with cocktail plastic cups. Measurements were conducted on days 2, 5, and 10. Females were freeze-killed for egg harvest and stored at -30°C until being dissected in distilled water using microdissection forceps to isolate and count eggs under a stereomicroscope (MZ95; Leica, Germany) at 2× magnification. Egg size was measured using a Dino-Lite digital camera (AM7115MZT-Edge, Dino-Lite, AnMo Electronics Corp., Hsinchu, Taiwan) by measuring the length and the diameter at the midpoint of its long axis of each mature egg. Only mature eggs were considered during the experiments (Iwata, 1959). Egg volume (µl) was estimated using the formula $V = (\pi r^2) (L-2r) + (4/3) (\pi r^3)$, where L= length, D= diameter and r=D/2 (O'Neill et al., 2014). In each treatment we had twelve individuals, except for *B. lissogaster*: water control on day 10, with six individuals, and for *B.* cephi: "PI 358716" IS-EFN on day 10; "Chinese red" and "PI 527281" LS-EFN on day 10, with respectively ten, eleven, and nine adult females.

Y-Tube olfactometer bioassays This bioassay was conducted to assess variation in behavioral responses of naïve females (Wäckers, 2004) to cowpea plant volatiles using the cultivars "Victor", "Chinese red", "PI 358716" and "PI 527281". Cowpea plants were 3-4 months old, 2-3 months after anthesis started. During the tests, we used an average of 11 leaves for “Victor”, and 23 leaves for the other smaller-leaved cultivars; green pods were present but inflorescences were not.

The Y-tube system (Analytical Research Systems, Micanopy, Florida, USA) is similar to that by (Piesik et al., 2008). Briefly, each arm of the Y-tube was connected to a diaphragm air pump that delivered charcoal-filtered and humidified air at a rate of 0.2 L/min. The Y-tubes consisted of Corning® glass tube (28-mm diameter x 300-mm long) that branched at 20 cm along in a 120° angle to form the arm of each tube. Each arm was 4 cm extended from the junction, becoming parallel arms that were 10-cm long. The end of each arm was connected to the air supply. Y-tubes were placed inside a black poster board box (46.0 x 32.0 x 101.5 cm) to prevent influence of ambient light. At the front portion of this box there were two holes, one providing light equally to both Y-tube arms by a fiber optic illuminator (T-Q/FOI-1, Techni QuipCorp, E1 Segundo, California, USA), and another hole where airstream was delivered by Teflon tubing (0.64-cm diameter). Individual plants were placed in a volatile collection chamber (100-mm diameter, 254-mm length), and connected by a 24/410 threaded glass joint to a Teflon tube to one end of the Y-tube, being alternated between assays. The bottom of the chamber was enclosed with a Teflon guillotine (995-mm diameter, and 15-mm center opening) (Analytical Research Systems, Micanopy, FL, USA).

To facilitate female movement towards the tube junction, a 28-cm long wire was placed on the unbranched portion of the Y-tube (from the introduction point to the junction). Females were placed inside the Y-tube on the top of the wire, 2 cm from the introduction point. Individuals were randomly assigned to each assay. Females were observed for 5 min and the trial ended when a choice was made, or individuals were considered a non-responder (whether they did not make a choice or returned to the beginning of the Y-tube). A total of 322 *B. cephi* were used during the trials, in which 61 females were used in bioassays with "Victor", 50 with "Chinese red", 111 with "PI 527281", and 100 with "PI 358716". We had a total of 239 *B. lissogaster*: 66 with "Victor", 67 with "Chinese red", 54 with "PI 527281", and 52 with "PI 358716". Non-responders were not considered for data analysis.

At the end of each bioassay, the glassware was cleaned using a non-foaming Alconox® detergent in warm water, rinsed with water, followed by the solvents acetone and hexane. Later, it was baked at 110°C in a glassware oven for at least 2 h before the next use.

Statistical Analysis

Statistical analyses were conducted in R (R Core Team, 2019) using RStudio (version 3.6.1). The effect of nectars or EFNs on longevity, egg load, and egg volume were tested using generalized mixed models, with blocks and individual plants treated as random effects. We also created a flattened variable by combining "cultivar" and "type of EFN". ANOVA tests with longevity and egg load were analyzed using the Poisson distribution family. Assumptions were checked by using diagnostic plots from car package (Fox and Weisberg, 2014), and model refinement was conducted based on stepwise deletion of terms based on the p-value ($p < 0.05$). Simple Pearson's chi-square tests were used to identify differences in parasitoid responses on tests with the odor sources of either the control airstream or cowpea volatiles tested in isolation ("Victor", "Chinese red", "PI 358716", and "PI 527281"). An alpha level of 0.1 was used to test for significant differences in female choices for both *B. cephi* and *B. lissogaster*.

Results

Longevity

Overall, both parasitoid species benefitted from IS-EFN and buckwheat nectar the most. *B. cephi* females lived an average of 10 days with water, and 17 days with LS-EFN, with an impressive increase to a 38-day average longevity with IS-EFN approaching that for buckwheat nectar at an average of 44 days. Meanwhile, *B. lissogaster* females followed the same pattern, surviving an average of 6 days with water, 17 days with LS-EFN, 28 days with IS-EFN, and 45 days with buckwheat nectar.

Our results show that there is an influence on longevity based on a 3-way interaction between the flattened variable “cultivar + type of EFN” – which combines plant cultivars and types of EFN–, species, and body size ($\chi^2_{(18,\ N= 268)} = 77.16$, $p < 0.001$), with *B. cephi* females living longer and being larger than *B. lissogaster* females. It also showed a 2-way interaction between “cultivar + type of EFN” and species ($\chi^2_{(9,\ N= 268)} = 92.77$, $p < 0.001$), where both species had the shortest lives when caged with water only and clearly displayed a substantial increase in longevity when caged with buckwheat nectar and cowpea EFN (Fig.3.1 and S1). All cowpea IS-EFN tended to better benefit parasitoid longevity when compared to both water and cowpea LS-EFN (Fig. 3.1), however, *B. lissogaster* females did not show differences between IS-EFN and LS-EFN for the cowpea cultivar “Chinese red” (Fig. 3.1). The statistical analyses were controlled for body size (tibia length), species, individual plants, and blocks (Table S3.1).

Egg Load and Egg Volume

B. cephi benefited from cowpea IS-EFN and buckwheat nectar when compared to the water control. These females produced 2.3-fold more eggs on buckwheat nectar, 2.1-fold more on cowpea IS-EFN, compared to a 1.2-fold increase on cowpea LS-EFN. In addition, egg volume increased 1.1-fold when provided cowpea LS-EFN, compared to a 1.8-fold increase with buckwheat nectar and 1.6-fold increase with IS-EFN. Interestingly, *B. lissogaster* females had a constant egg load and egg volume across treatments.

Egg load varied based on an interaction between body size and cumulative days of feeding, where body size had more influence on egg load on days 2 and 5 when compared to day 10, and with bigger females having more eggs ($\chi^2_{(2, N=708)} = 9.09$, $p = 0.011$, Fig. S3.2). We also noticed that *B. lissogaster* had more eggs than *B. cephi*, with greater numbers on days 2 and 5, compared to day 10, while *B. cephi* had fewer eggs on day 2 than days 5 and 10 ($\chi^2_{(2, N=708)} = 28.71$, $p < 0.001$, Fig. 3.2, Fig. S3.3). We found strong evidence suggesting variation in egg load based on 2-way interaction between the flattened variable "cultivar + type EFN" and species ($\chi^2_{(9, N=708)} = 82.59$, $p < 0.001$, Fig. 3.2). *B. lissogaster* egg load did not vary across the different plant cultivars and types of EFN, while *B. cephi* had the most eggs when fed on buckwheat nectar and cowpea IS-EFN, except for the cowpea cultivar "Chinese red" which had similar larger values for IS-EFN and LS-EFN than for water (Fig. 3.2 and Table S3.2).

We did not find evidence of an influence of cumulative days of feeding on egg volume in either species ($\chi^2_{(2, N=708)} = 2.78$, $p = 0.249$). However, egg volume changed based on an interaction between the flattened variable "cultivar + type EFN" and species ($\chi^2_{(9, N=708)} = 73.61$, $p < 0.0001$, Fig 3.3). As observed for egg load, *B. lissogaster* egg volume did not vary based on the different treatments, but *B. cephi* had greater egg volume when fed on cowpea IS-EFN and buckwheat nectar when compared to both water and cowpea LS-EFN. As for egg load, the cowpea cultivar "Chinese red" resulted in similar egg volumes that were greater than with water, whether IS-EFN and LS-EFN was accessed (Fig 3.3 and Table S3.2). There was variation in egg volume based on an interaction between body size and cumulative days of feeding ($\chi^2_{(2,\ N= 708)}$ = 23.08, p < 0.0001, Fig. S3.4), with body size more strongly influencing egg volume on day 2 compared to days 5 and 10. Bigger females also had bigger eggs, and *B. cephi* had bigger eggs than *B. lissogaster* ($\chi^2_{(1,\ N= 708)}$ = 9.89, p-value = 0.001, Fig. 3.3, Fig. S3.5).

The statistical analyses conducted for egg load and egg volume had the flatten variable combining the plant cultivars and the types of EFN (cultivar + type of EFN), body size, species, and cumulative days of feeding as additive variables. The model also controlled for individual plants and blocks (Table S3.1).

Behavioral Experiments

Adult females responded positively towards airstreams containing cowpea volatiles for both *B. cephi* ($\chi^2_{(1,\ N= 322)}$= 9.74, p = 0.001) and *B. lissogaster* ($\chi^2_{(1,\ N= 239)}$= 10.88, p < 0.001), when compared to "Pure air". A greater number of *B. lissogaster* females chose airstreams passing over the cowpea lines "PI 358716" ($\chi^2_{(1,\ N= 52)}$= 7.69, p = 0.005) and "Chinese red" ($\chi^2_{(1,\ N= 67)}$= 4.31, p = 0.038), when the choices were between the individual cowpea lines or "Pure air" (Fig. 3.4 and Table S3.3). *B. cephi* females preferred airstreams passing over the cowpea line "Chinese red" ($\chi^2_{(1,\ N= 50)}$ = 8.00, p = 0.004), when the choices were "Chinese red" and "Pure air" (Fig. 3.4 and Table S3.3), and has a significant positive response for airstream passing over the cowpea line “PI 358716” when compared to “Pure air” ($\chi^2_{(1, N= 100)}$= 3.24, p = 0.071). *B. cephi* and *B. lissogaster* did not make choices in response to the airstreams passing over the individual cowpea lines “Victor” (*B. cephi*, $\chi^2_{(1, N= 61)}$= 1.33, p = 0.249; *B. lissogaster* $\chi^2_{(1, N= 67)}$= 0.97, p = 0.325), and “PI 527281” (*B. cephi*, $\chi^2_{(1, N= 111)}$= 0.73, p = 0.393; *B. lissogaster* $\chi^2_{(1, N= 54)}$= 0.67, p = 0.414).

Discussion

Here we show that an exotic cover crop with accessible nectar source can potentially enhance ecosystem services from native specialist species that parasitize a recently adapted pest in large areas of intensified agriculture. Greater longevity and increased egg productivity are extremely important for landscape scale populations of a pest across depauperate dryland agriculture. *Bracon cephi* and *B. lissogaster*, the two most important parasitoid species of wheat stem sawfly, are synovigenic and can benefit from nectar availability by increasing longevity and fecundity, and, consequently, increasing their potential success as biological control agents as has been found for other species (Jervis et al., 2008; Manandhar and Wright, 2016). The wheat stem sawfly is the only known host of both species, so they are extremely specialized. In this study, we observed that adult parasitoid females feeding on buckwheat nectar and cowpea IS-EFN had increased longevity, with *B. cephi* females also increasing egg load and egg volume. Even though *B. lissogaster* females did not show differences in reproductive parameters based on the different treatments, they were able to keep a constant egg load and volume throughout their adult life span when feeding on nectar and water.

Influence of EFN on Longevity, Egg Load and Egg Volume

Artificial carbohydrate-rich diets increase longevity on *B. cephi* and *B. lissogaster* (Reis et al., 2019; Cavallini et al., 2022 – Submitted). When feeding on buckwheat nectar, *B. cephi* also increases longevity (Rand and Waters, 2020; Reis, 2018). As expected, our results show that both braconid parasitoids increased longevity when fed buckwheat nectar or cowpea EFN. Our results also show that egg load and egg volume were increased for *B. cephi* when feeding on buckwheat nectar (Rand and Waters, 2020; Reis, 2018), and also when feeding on cowpea IS-EFN, which is advantageous given that egg size is linked to offspring fitness (Giron and Casas, 2003).

Females fed water and cowpea LS-EFN displayed the lowest longevity, with *B. cephi* also having lower egg load and egg volume than *B. lissogaster*. This result suggests that, even though *B. cephi* females have shorter lifespans and have smaller eggs, they invest adventitiously consumed resources in their eggs. As a consequence, they increase the probability of progeny survival (Allen et al., 2008; Fox and Czesak, 2000; Muller et al., 2017). Meanwhile, *B. lissogaster* egg load and volume did not change based on the cowpea and buckwheat treatments, which is an interesting outcome given that females live shorter periods when with water but kept the number and size of eggs constant, independent of the food resource. We also noticed that older females of *B. lissogaster* decreased the number of eggs they carried, most likely because they are producing fewer eggs and/or they are resorbing eggs. Synovigenic parasitoids can resorb mature eggs when food resources are not widely available, and, thus, they reallocate energy for maintenance and longevity instead (Rivero and Cass 1999).

As noticed for longevity, females feeding on LS-EFN had lower egg load and egg volume compared to buckwheat nectar and IS-EFN, and this result can be due to feeding frequency. During our experiments, the amount of extrafloral nectar being produced by cowpea leaf stipels was visibly smaller than for inflorescence stalks, and, thus, females fed cowpea LS-EFN might have been impaired by reduced feeding frequency due to a longer wait for droplets to form anew. In a related species, braconid parasitoid adults perform better when fed supplemental nutrients daily rather than every other day (Azzouz et al. 2004). Meanwhile, the koinobiont braconid *Cotesia rubecula* (Marshall) avoids starvation by feeding at least once per day, depending on the amount of sugar present in the food resource (Siekmann et al., 2001). In addition, the oogenesis process is dependent on the adult female fat body, where resources may come from reserves accumulated during larval host feeding and also from additional supplemental nutrients acquired as adults (Rivero and Casas, 1999).

Importance of EFN Composition

Longevity in parasitoids increases when they are fed carbohydrate-rich resources, such as buckwheat nectar and honeydew (Lee et al., 2004). Vattala et al. (2006) noticed that parasitoids live longer when they are fed sucrose-rich nectar, which is the case for both buckwheat nectar (Tompkins et al., 2010; Vattala et al., 2006) and cowpea EFN (Pate et al., 1985). As expected, *B. cephi* and *B. lissogaster* lived longer when fed on buckwheat nectar or cowpea IS-EFN. These greenhouse results build on other lab studies where both *B. cephi* and *B. lissogaster* increased longevity when fed artificial carbohydrate-rich diets (Reis et al., 2019; Cavallini et al., 2022 – Submitted).

Females feeding on cowpea LS-EFN did not benefit compared to those that were fed buckwheat nectar or cowpea IS-EFN. An explanation for this is EFN composition, where the two types of cowpea EFN differ, with LS-EFN having lower amino acid-sugar balance, fewer nitrogenous solutes and organic acids, but more monosaccharides when compared to IS-EFN (Pate et al., 1985). Carbohydrate-rich diets can increase the levels of osmotic stress in insects, including glucose and fructose dominant nectars (Ashford et al., 2000; Vattala et al., 2006). Therefore, it is possible that the female parasitoids fed cowpea LS-EFN experienced challenges in maintaining homeostasis due to less-than-optimal sugar concentrations, leading to osmoregulatory dysfunction and associated physiological constraints (Vattala et al., 2006). Nectar has other compounds that could influence parasitoid longevity, and these compounds could be of greater influence in longevity than the sugar content itself (Tompkins et al. 2010). Second, there are potential limitations due to LS-EFN taste, where an increased amino acid ratio or the presence of other metabolites can confer unpleasant taste to the nectar (Nepi, 2014; Price et al., 2011). High concentrations of secondary metabolites in nectar increase the rejection by feeders (Köhler et al., 2012), and therefore could be reducing the amount of EFN consumed by these braconid parasitoids.

Essential amino acids positively affect fecundity compared to a restricted diet comprised of carbohydrates, vitamins, and lipids in *Drosophila melanogaster* Meigen females (Grandison et al., 2009). This, together with the differences observed when females were fed cowpea IS-EFN or LS-EFN, suggests that longevity, egg load, and volume are being influenced by nectar content. Cowpea LS-EFN has more monosaccharides but less amino acids and organic acids than

IS-EFN (Pate et al. 1985). Therefore, the availability of nutrients, especially amino acids in nectar, might allow female parasitoids to allocate resources towards egg production for longer periods of time.

Behavioral Experiments

The close-range attraction of insects to nectar is related to its composition and sucrose ratio, which can change across and within plants (Jervis et al., 1993). Parasitoids use certain plant traits, such as volatile compounds (odor) and flower color to find food sources (Belz et al., 2013; Wäckers, 2004). Our results show that both *B. cephi* and *B. lissogaster* are innately attracted to volatiles from cowpea plants and can use cowpea EFN as a food source.

Innate vs learned responses

In this research, we tested naïve parasitoids that did not have any previous experience or association of visual or olfactory cues to the EFN reward. Therefore, the responses observed were innate and driven entirely by host plant compounds. The presence and availability of nectar are not sufficient to induce innate attraction in parasitoids, even when they are food-deprived (Wäckers, 2004). Therefore, other traits, such as plant odor, play important roles in attraction by these parasitoids. Our results reveal that *B. cephi* and *B. lissogaster* are innately attracted to cowpea odor, which is interesting given that cowpea is an exotic species, not present in Montana, and infrequently sown on the Northern Great Plains.

Parasitoids use visual and olfactory cues to learn and modify their behavioral responses (Lewis et al., 1998). Some parasitoid species readily perceive EFN and are highly attracted to it (Stapel et al., 1997). Once they successfully find and feed on EFN, they might associate visual and olfactory cues to this reward (Lewis et al., 1998; Wäckers and Lewis, 1994). Previous experiences affect the kind of food source on which parasitoids are going to choose to feed (Makatiani et al. 2014). We did not test if *B. cephi* and *B. lissogaster* female responsiveness changes based on previous experiences, but because all tested individuals were naïve, there is a possibility that these females will be more attracted to cowpea odors after exposure to these EFNs as a food reward. The eulophid parasitoids *Edovum puttleri* Grissell and *Pediobius foveolatus* Crawford had increased attraction to nectar odors after foraging experiences in dill flowers (Patt et al., 1999), and *M. croceipes* increases attraction to cotton after EFN exposure (Röse et al., 2006). Therefore, investigating initial plant attractiveness to natural enemies is a critical step in conservation biological control, especially in highly specialized systems.

Conclusion

The selection of plants as food source for beneficial insects depends on the resource accessibility by these insects, which in turn confers benefits in longevity and reproductive parameters, such as egg load and egg volume (Gurr et al., 2017; Landis et al., 2000). Extrafloral nectar benefits insects for longer periods of time because it is not flower dependent (Heil et al., 2004). Ideally, in conservation biocontrol programs, parasitoids should have food available early in the season, and as observed during our experiments, cowpea produces EFN steadily once leaves form. Moreover, our findings indicate that naïve parasitoids are already attracted to cowpea odors which is promising for the use of this potential cover crop in conservation biological control of wheat stem sawfly. Complementary studies are needed to better understand the effects of cowpea EFN and volatile compound blends on both *B. cephi* and *B. lissogaster*, particularly after field conditioning to EFN and associated learned behaviors has occurred.

When implementing conservation biocontrol, the selected plant species must also be viable for growers to readily cultivate (Landis et al., 2000). The use of flowering cover crops in habitat management benefits cultivated land because it increases soil nitrogen, reduces soil erosion (Crews and Peoples, 2005), suppresses weeds (Mhlanga et al., 2016; Weisberger et al., 2019), and reduces pest pressure while increasing yields in agroecosystems (Bullock, 1992; Kirkegaard et al., 2008; Miller et al., 2002). Our findings for these native parasitoids show that cowpea matches the fundamental criteria necessary to be considered as a food supplement for conservation biocontrol programs of major pests (in this case wheat stem sawfly), such as food availability, plant attractiveness, food accessibility, and nutritional benefits to our natural enemies (Wäckers, 2005). We encourage more research to further investigate cowpea agronomic performance at the field level for the Northern Great Plains while carefully observing for any additional benefits to diverse crop and wildland entomofauna. Our efforts suggest a different path for considering how conservation biological control might be accomplished across large areas of depauperate cropland, where specialists critical to key pest suppression are considered while evaluating crops that could be used to add resilience. The need for ecosystem services is necessarily predicated by pollinator considerations, but most pollinators are much more effective at accessing nectar from a diversity of crop plants. In contrast, parasitoids are constrained to far fewer species that provide accessible nectar and consideration of extrafloral nectar producing crops could be prioritized for conservation biological control centered on parasitoids.

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Figures

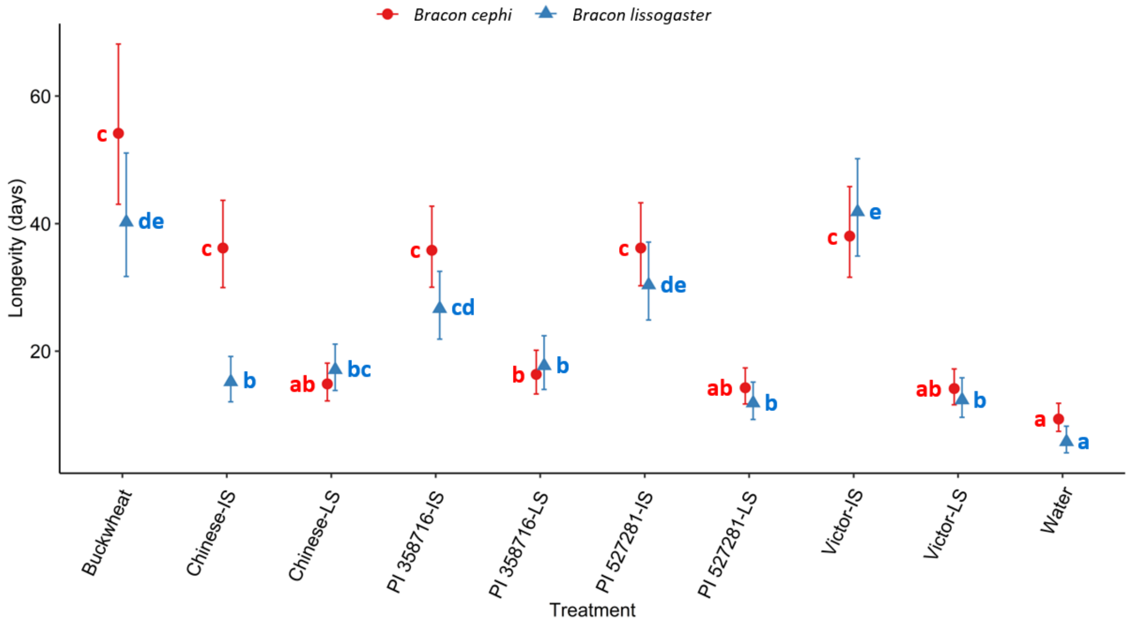

Fig. 3. 1. Effects on longevity, represented as means and SEs, of adult female feeding on different types of extrafloral nectar (IS representing Inflorescence Stalk EFN, and LS representing Leaf Stipel EFN) and cowpea cultivars (“Victor”, “Chinese red”, “PI 358716”, or “PI 527281”) for both *Bracon cephi* and *B. lissogaster*.

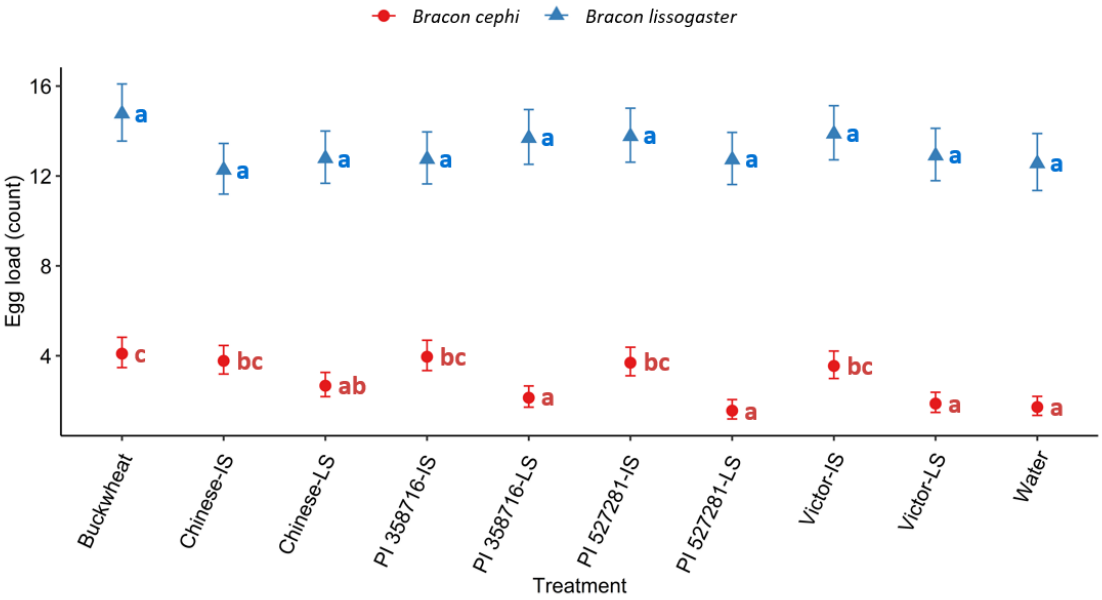

Fig. 3. 2. Predicted values represented as means and SEs for the mean egg load of *Bracon cephi* and *B. Lissogaster* based on cowpea cultivars (“Victor”, “Chinese red”, “PI 358716”, or “PI 527281”) and type of extrafloral nectar, with IS representing inflorescence stalk EFN, and LS representing leaf stipel EFN.

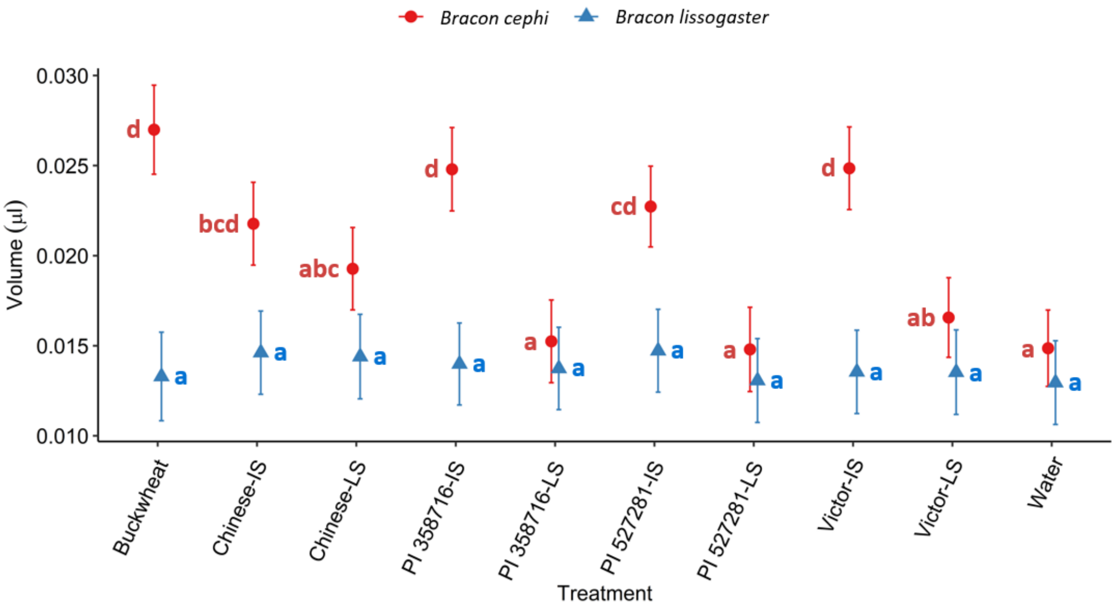

Fig. 3. 3. Effects represented as means and SEs on mean egg volume (µl) of *Bracon cephi* and *B. lissogaster* females based on different cowpea cultivars ("Victor", "Chinese red", "PI 358716", or "PI 527281") and type of extrafloral nectar, with IS representing inflorescence stalk EFN, and LS representing leaf stipel EFN.

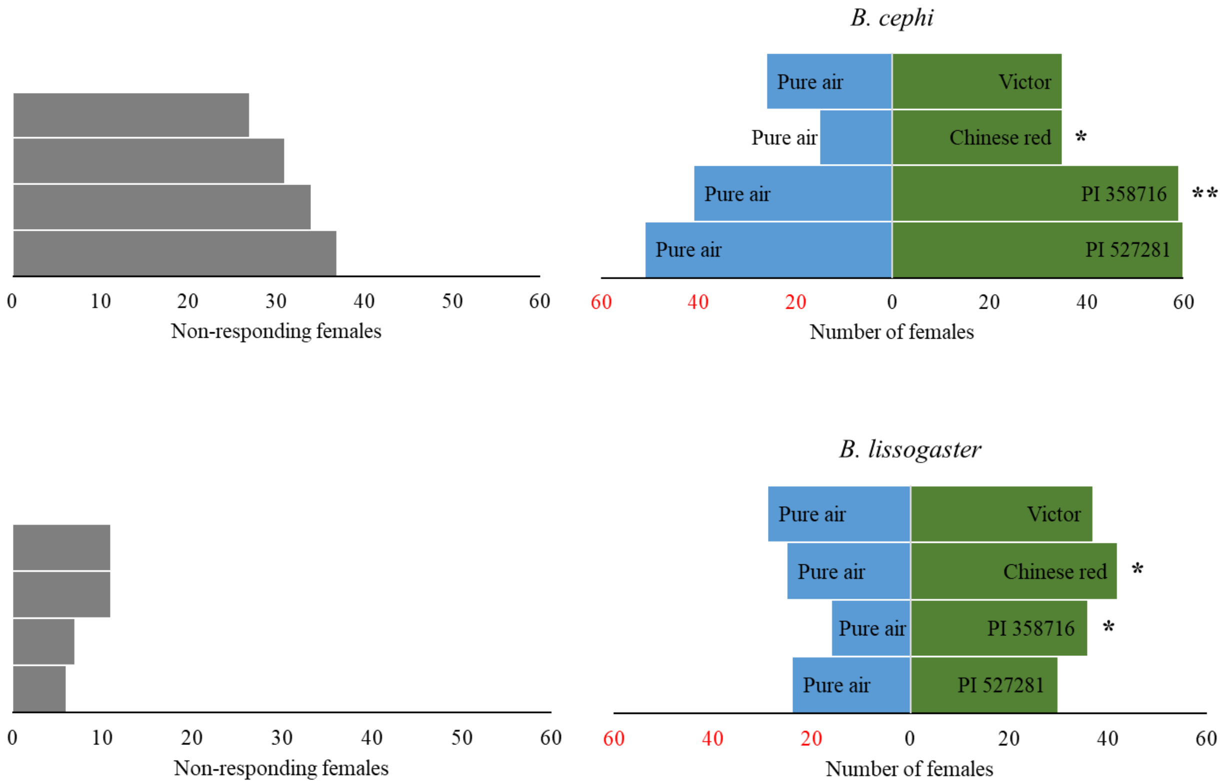

Fig. 3. 4. Preferences from Y-tube olfactometer tests for both *Bracon cephi* and *B. lissogaster* females when choosing between “Pure air” and one of the cowpea cultivars “Victor”, “Chinese red”, “PI 358716”, or “PI 527281”. Left side bar graphs show the number of non-responder females related to trials with the different cowpea cultivars. * represents $p \leq 0.05$ and ** $p < 0.075$ on Pearson’s Chi-square test.

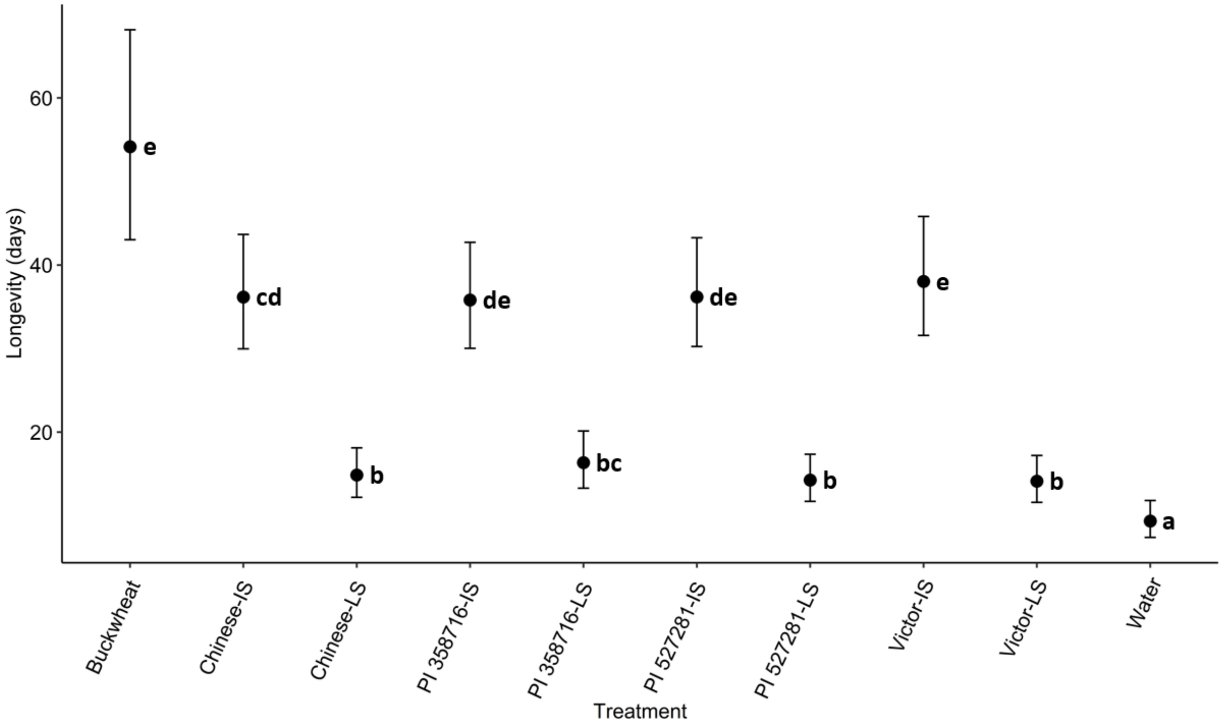

Fig S3. 1. Predicted values of mean estimated longevity and CIs for pooled individuals of female parasitoids of both species fed on two types of cowpea EFN (IS representing Inflorescence Stalk EFN, and LS representing Leaf Stipel EFN) and the different cowpea cultivars (“Victor”, “Chinese red”, “PI 358716”, or “PI 527281”). Groups with same letter are not different in pairwise comparison tests, with a 5% familywise significance level.

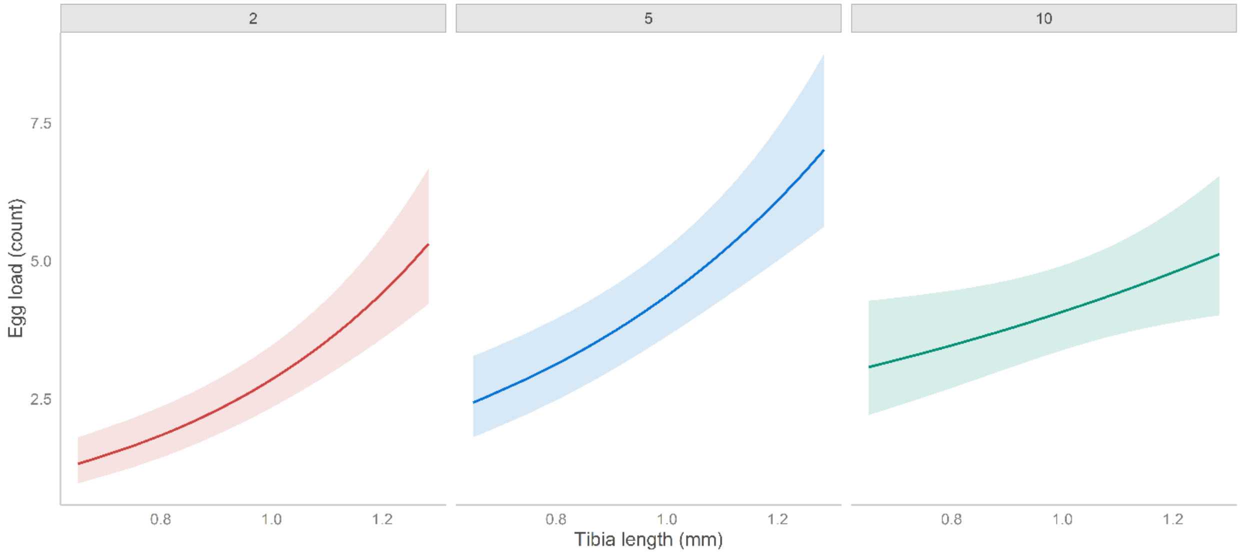

Fig S3. 2. Effect plot displaying predicted values of mean egg load based on interactions between parasitoid females' body size (tibia length in mm, pooled for *Bracon cephi* and *B. lissogaster*) and the three days where cumulative feeding effects were measured.

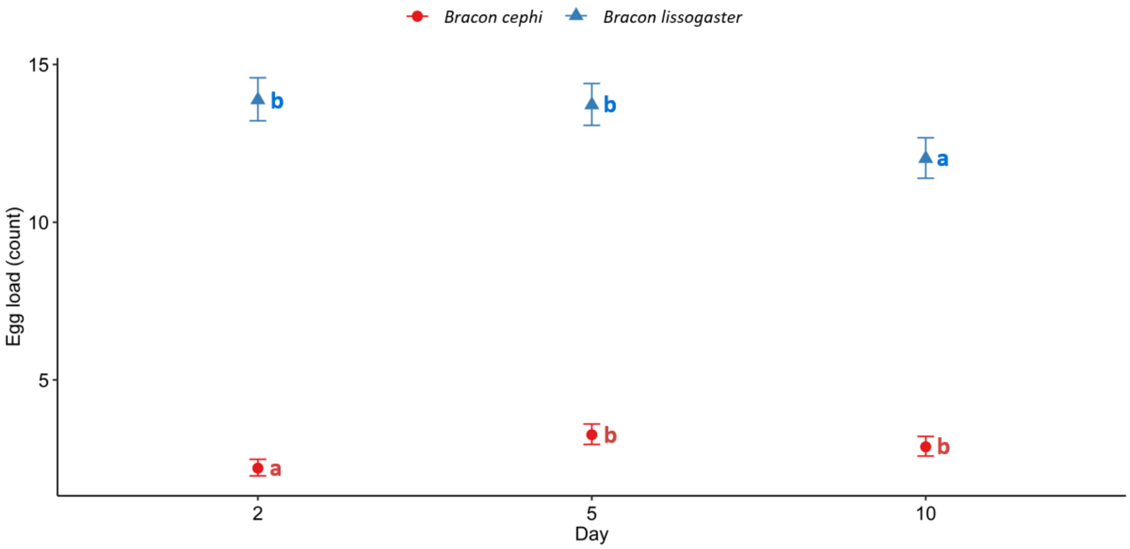

Fig S3. 3. Predicted values of mean egg load and CIs for *Bracon cephi* and *B. lissogaster* females for the three days where cumulative feeding effects were measured on pooled cowpea cultivars. Groups with same letter are not different in pairwise comparison tests, with a 5% familywise significance level

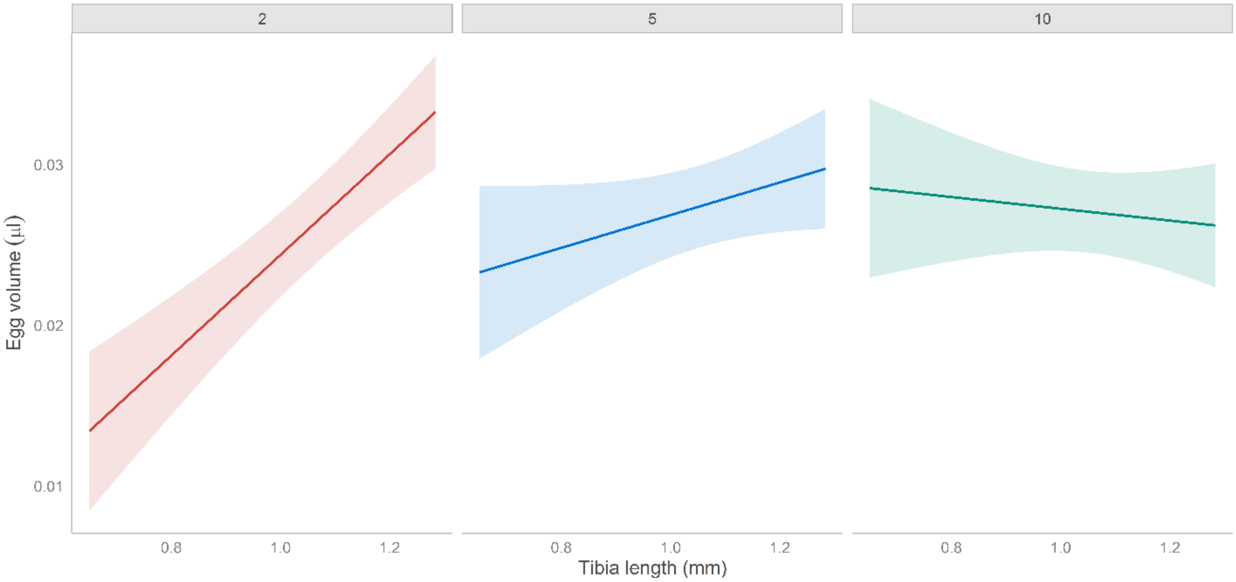

Fig S3. 4. Effect plot displaying predicted values of mean egg volume based on interactions between parasitoid females' body size (tibia length in mm) and the three days where cumulative feeding effects were measured. Data is pooled for *Bracon cephi* and *B. lissogaster* females.

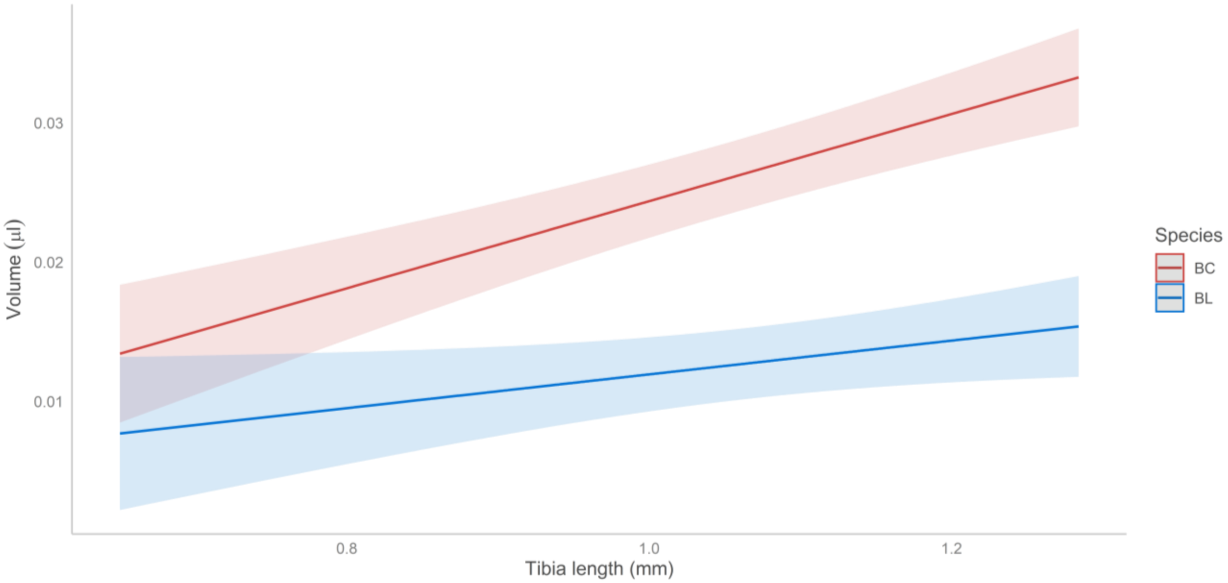

Fig S3. 5. Effect display of the interaction between *Bracon cephi* (BC) and *B. lissogaster* (BL) females and body size (tibia length in mm), based on a logit model fit for egg volume (µl).

Tables

Table S3. 1. Results of the statistical analysis conducted for longevity, egg load, and egg volume for females of *Bracon cephi* and *B. lissogaster*, using the flattened variable "Cultivar + Type of EFN". * represents interaction between the variables.

Longevity			
Variable	**$\chi 2$**	**Df**	**p-value**
Cultivar and Type of EFN	677.38	9	< 0.0001
Tibia	20.81	1	0.0001
Species	7.24	1	0.0071
(Cultivar and Type of EFN) * Species	97.77	9	0.0000
Tibia * Species	0.41	1	0.5221
(Cultivar and Type of EFN) * Tibia * Species	77.16	18	0.0001
Egg load			
Cultivar and Type of EFN	39.96	9	< 0.0001
Day	17.70	2	0.0001
Tibia	82.73	1	< 0.0001
Species	1787.06	1	< 0.0001
(Cultivar and Type of EFN) * Species	82.59	9	< 0.0001
Day * Tibia	9.09	2	0.0106
Day * Species	28.71	2	< 0.0001
Egg volume			
Cultivar and Type of EFN	78.81	9	< 0.0001
Day	2.78	2	0.2493
Tibia	5.02	1	0.0250
Species	160.25	1	< 0.0001
(Cultivar and Type of EFN) * Species	73.61	9	< 0.0001
Day * Tibia	23.08	2	< 0.0001
Tibia * Species	9.89	1	0.0017

Table S3. 2. Results of calculations for the percentage increases when compared to water in both egg load and volume for *Bracon cephi* and *B. lissogaster*. Measurements were conducted on different cowpea cultivars (“Victor”, “Chinese red”, “PI 358716”, or “PI 527281”) and both IS-EFN or LS-EFN for 2, 5, and 10 days. Buckwheat was used as a positive control.

	Bracon cephi					
	Egg Volume (%)			**Egg Load (%)**		
	Day			**Day**		
	2	**5**	**10**	**2**	**5**	**10**
Buckwheat	112	91	44	141	152	92
Cowpea I-EFN						
PI 527281	49	71	32	59	135	100
PI 358716	93	68	41	76	117	164
Chinese	67	54	28	100	117	116
Victor	86	86	40	94	152	64
Cowpea L-EFN						
PI 527281	34	15	43	-18	13	-36
PI 358716	32	7	15	94	4	-8
Chinese	58	45	2	124	43	9
Victor	33	41	31	12	57	-44

	Bracon lissogaster					
	Egg Volume			**Egg Load**		
	Day			**Day**		
	2	**5**	**10**	**2**	**5**	**10**
Buckwheat	21	7	10	8	20	28
Cowpea I-EFN						
PI 527281	18	17	7	10	17	21
PI 358716	10	8	7	4	9	2
Chinese	7	35	5	1	10	2
Victor	11	8	7	11	14	22
Cowpea L-EFN						
PI 527281	1	7	9	5	-1	10
PI 358716	-10	31	5	-5	30	3

Table S3. 2 Continued

Chinese	17	14	10	16	-11	12
Victor	10	13	4	5	3	12

Table S3. 3. Response of both *Bracon cephi* and *B. lissogaster* females to airstream containing volatiles emitted by cowpea in Y-tube olfactometer test. Females had the option to choose between pure air or one of the sole cowpea cultivars "Victor", "Chinese red", "PI 358716", and "PI 527281".

Bracon cephi

	Choice		**Behavioral responses**	
	Cowpea	**Pure air**	**χ2**	**p-value**
Victor	35	26	1.33	0.249
Chinese red	35	15	8.00	**0.004**
PI 358716	59	41	3.24	**0.071**
PI 527281	60	51	0.73	0.393

Bracon lissogaster

	Choice		**Behavioral responses**	
	Cowpea	**Pure air**	**χ2**	**p-value**
Victor	37	29	0.97	0.325
Chinese red	42	25	4.31	**0.038**
PI 358716	36	16	7.69	**0.005**
PI 527281	30	24	0.67	0.414

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CHAPTER FOUR

CONCLUSION

Our research assessed the effects of carbohydrate- and amino acid-rich artificial diets, as well as cowpea extrafloral nectar as food resources for *Bracon cephi* and *B. lissogaster*, native parasitoids of wheat stem sawfly, *Cephus cinctus*. We repeatedly observed broad benefits of supplemental nutrition on the longevity of *B. cephi* and *B. lissogaster*, as well as for egg load, and egg volume of *B. cephi*. In addition, we also assessed whether there was an innate, adventitious attractiveness to cowpea in these parasitoids. This information is critical for the improvement of conservation biocontrol programs to reduce wheat stem sawfly populations.

We evaluated the effects of carbohydrate-rich diets, both in combination with amino acids and alone, for *B. cephi* and *B.* lissogaster. Both species increased longevity with carbohydrate-rich diets, with glucose highly benefitting longevity when compared to other treatments. *B. cephi* females increased egg load and egg volume when fed carbohydrates, especially during the initial 5 days of adult life. We noticed that *B. cephi* females tend to increase egg load and egg volume when there is an addition of amino acids to the diets. The number of females available for use in each experiment depends on population density and species composition for different locations, so we were not able to analyze egg load and egg volume for *B. lissogaster* during this study.

We investigated the effects of both cowpea inflorescence stalk extrafloral nectar (IS-EFN) and leaf stipel extrafloral nectar (LS-EFN) on the longevity, egg load and egg volume of *B. cephi* and *B. lissogaster*. Our results revealed that both species can access and feed on cowpea

EFN, with IS-EFN improving longevity for both species. Interestingly, supplemental nutrition did not impact egg load and egg volume in *B. lissogaster*, but *B. cephi* increased these reproductive parameters when fed cowpea IS-EFN.

Cowpea is an exotic plant species unfamiliar to our parasitoids, and thus there was the need to test if adult females would be attracted to its odors. This is plausible because volatile compounds are highly conserved across species and serve a variety of roles in plant-insect communication. Both parasitoid species were strongly attracted to "Chinese red", while *B. lissogaster* was strongly attracted to "PI 358716" and *B. cephi* being less strongly attracted to this cultivar. Importantly, none of the female parasitoids was averse to cowpea odor.

B. cephi and *B. lissogaster* are both synovigenic specialist ectoparasitoids, that feed on the same host and share the same locations. Hence, one could expect them to have the same nutritional requirements and reproductive behavior. Our results reveal that this is not the case. *B. cephi* produces fewer eggs than *B. lissogaster*, but they are bigger. Moreover, *B. lissogaster* did not change egg load and volume based on diets, while *B. cephi* enhanced these reproductive parameters on carbohydrate rich resources. Interestingly, during our studies we did not notice consistency in species composition across locations. This was likely related to intrinsic differences in the fields where we collected wheat residue. More studies are needed to clarify the interactions between these two parasitoids at the field, and to determine the potential influence of abiotic factors on their populations.

By exploring these specific nutritional requirements for longevity and reproduction from supplemental sources, it is possible to envision a more successful biological control program for wheat stem sawfly. Ideally, in these programs, parasitoids should have food available early and also quite late in the season. Cowpea is advantageous because, as observed during our experiments, EFN are available as soon as leaves started to form and both types of EFN were continually present until cold conditions caused senescence. Availability of cowpea EFN is important for these parasitoids because early in the season individuals that overwinter need to restore nutrition. These parasitoids also need additional resources to host-seek, which is especially challenging later in the season when wheat stem sawfly larvae are present in reduced numbers due to wheat maturity and desiccation.

In conclusion, our study reveals the nutritional needs for both *B. cephi* and *B. lissogaster*, showing the benefits of supplemental nutrition on their longevity, egg load, and egg volume. Moreover, we suggest that cowpea is a promising candidate in conservation biocontrol programs in wheat stem sawfly, because *B. cephi* and *B. lissogaster* females are attracted to cowpea volatiles, and cowpea EFN are plentifully available, easily accessible, and provides nutritional benefits to both parasitoid species. However, we need a better understanding of cowpea agronomic performance at the field level and to document any benefits to a diverse crop and wildland entomofauna. In addition, it would be of great benefit to investigate how floral and extrafloral nectar and its composition, affect these parasitoids and their success in managing wheat stem sawfly populations on the landscape.

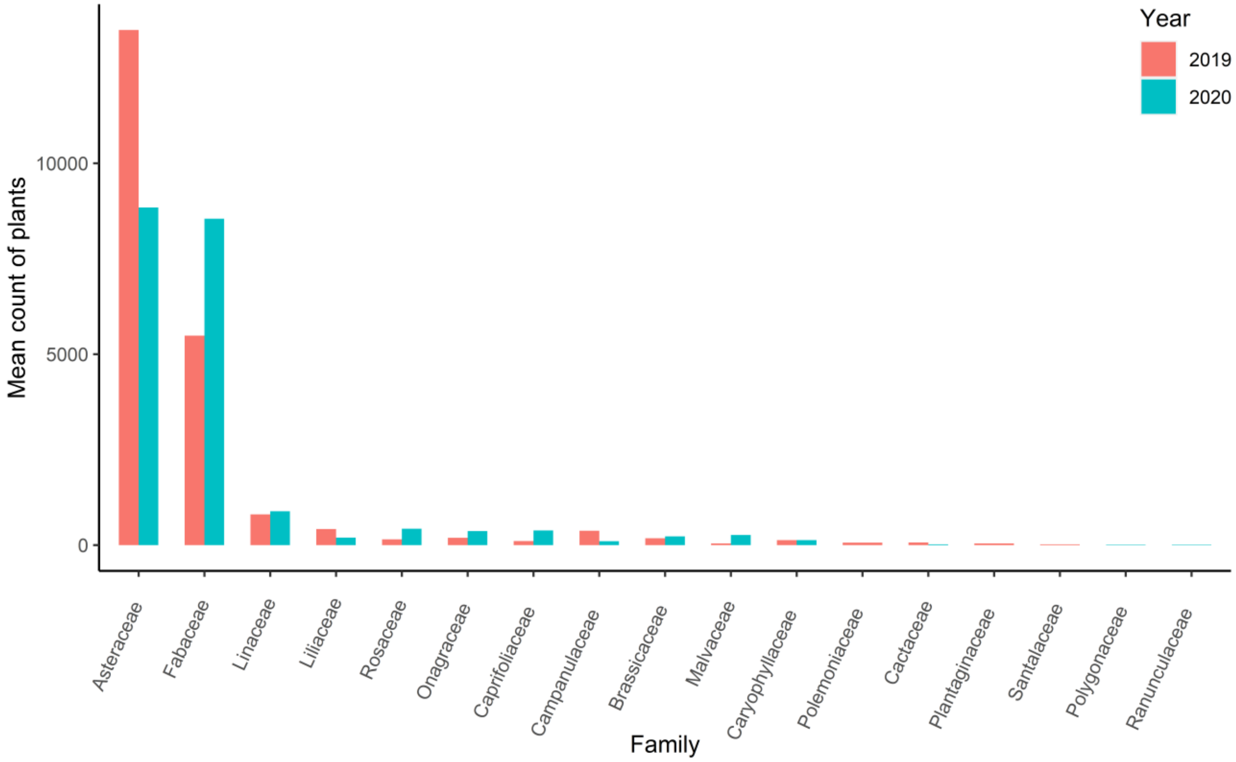
APPENDICES

<u>APPENDIX A</u>

ASSESSING WILDLAND FLOWERING SPECIES TO IMPROVE BIOCONTROL STRATEGIES OF WHEAT STEM SAWFLY IN MONTANA

The use of non-crop habitats in agroecosystems can increase landscape diversification and provide a safer place for insects where there is tillage, harvest, or insecticide application (Chakraborty et al., 2017; Gurr et al., 2017; Landis et al., 2000). It can also provide shelter and food resources for natural enemies (Adhikari et al., 2018; Gurr et al., 2017; Landis et al., 2000; Perović et al., 2018). The use of flower strips increases natural enemy abundance, contributing to pest management (Tschumi et al., 2015; Tylianakis et al., 2004; Wäckers and van Rijn, 2012). Wildflower strips provide high amounts of floral resources and attract aphid predators in apple orchards (Santos et al. 2018). Amy et al. (2018) compared multifloral and monofloral strips adjacent to winter wheat, showing that a wider range of flowering plants further increase the diversity of pollinators and natural enemies. In addition, non-prey foods provide nutrients that can increase natural enemies' abundance (Patt et al., 1997; White et al., 1995) and rates of parasitism in parasitic arthropods (Lee and Heimpel, 2008; Stephens et al., 1998). These nutrients contribute to egg maturation (Jervis and Kidd, 1986), enhancing the efficacy of biological control agents (Jervis et al., 1993). Many studies showed that availability of food increases parasitoid longevity (Reis et al., 2019; Wäckers, 2001), fecundity (Idris and Grafius, 1995; Tylianakis et al., 2004; Winkler et al., 2006), and activity (Stapel et al., 1997; Takasu and Lewis, 1995). As is the case for *Bracon cephi* and *B. lissogaster*, which have been recorded to increase longevity, egg load, and volume when fed artificial sucrose solutions (Reis et al., 2019).

Knowing the benefits that floral resources can have for agricultural landscapes, and, more specifically, the effects of food sources availability in longevity and reproductive biology in both *B. cephi* and *B. lissogaster*, our study had the objective of assessing and identifying wildland flowering species that could be used as floral resources in agricultural landscapes in Montana. For that, surveys were conducted on a 12-ha rangeland area near Havre, Montana, USA during the summer of 2019 and 2020. Visits were made twice per month, from June to September, to catalogue the observed flowering species. We used 10-m wide transects to cover the whole area, with sampling being conducted in every other transect. We observed a total of 21,560 plants and 53 different flowering species in 2019, and 20,414 plants and 50 different species in 2020 (Appendix A, Table 1). Most plant species were native, mainly belonging to the families Asteraceae and Fabaceae (Appendix A, Fig. 1). To better analyze the data set, we picked the 10 most abundant plant species observed for each month (Appendix A, Table 2). There are similarities when comparing the "top 10" species in both years, with plants usually flowering about the same month each year. This is relevant given that *B. cephi* and *B. lissogaster* are active and parasitizing wheat stem sawfly immatures from June to September. Hence, food resources must be available during these months to benefit these natural enemies. Based on our "top 10" species for both years, we identified 20 different native species that could be tested as food sources on flower strips, including *Achillea millefolium* L., *Artemisia cana* Pursh., *Aster falcatus* Lindl., *Cerastium arvense* L., *Dalea purpurea* Vent., *Gaura coccinea* Pursh., *Gutierrezia sarothrae* Pursh., *Helianthus annuus* L., *Heterotheca villosa* Pursh, *Liatris punctata* Hook., *Linum lewisii* Pursh, *Lygodesmia juncea* Pursh., *Pediomelum argophyllum* Pursh, *Ratibida columnifera* Nutt., *Rosa arkansana* Porter, *Solidago missouriensis* Nutt., *Solidago mollis* Bartl., *Vicia americana* Muhl., *Xanthisma spinulosum* Pursh, *Zigadenus venenosus* S. Watson. We believe that these plant species could offer nectar for *B. cephi* and *B. lissogaster*, possibly contributing to their success as natural enemies before agricultural intensification. Moreover, nectar access might be critical for these braconid parasitoids success as natural enemies because, first, these individuals overwinter and need to restore their nutritional reserves early in the season. Second, later in the season, wheat stem sawfly larvae are present in reduced numbers due to wheat maturity and desiccation, therefore, parasitoids can benefit from a boost in energy reserves to find its host. Our results show plant species that could be used in flower strips adjacent to wheat fields in Montana. However, further work is required to understand the potential of flower strips in improving wheat stem sawfly biocontrol and wheat yield. In addition, there is a need to investigate if nectar is accessible to *B. cephi* and *B. lissogaster*, and if the resource availability is not benefitting wheat stem sawfly.



Appendix A, Fig. 1. Display of the mean count of plants based on family for the 2019 and 2020 sampling years.

Appendix A, Table 1. Total numbers of flowering plants observed for each species during 2019 and 2020 sampling years.

2019		**2020**	
Species	**Number of individuals**	**Species**	**Number of individuals**
Achillea millefolium	2206	***Achillea millefolium***	1945
Allium textile	34	***Allium textile***	20
Artemisia cana	1706	***Anemone multifida***	11
Aster falcatus	2246	***Arnica sororia***	2
Astragalus adsurgens	116	***Artemisia cana***	710
Astragalus crassicarpus	3	***Aster falcatus***	37
Astragalus gracilis	162	***Astragalus gracilis***	41
Campanula rotundifolia	374	***Campanula rotundifolia***	101
Cerastium arvense	69	***Cerastium arvense***	84
Cirsium arvense	60	***Cirsium arvense***	45
Cirsium undulatum	21	***Cirsium undulatum***	51
Comandra umbellata	18	***Crepis occidentalis***	18
Crepis acuminata	7	***Dalea purpurea***	465
Crepis occidentalis	5	***Erigeron caespitosus***	60
Dalea purpurea	308	***Erigeron ochroleucus***	20
Erigeron caespitosus	74	***Eriogonum umbellatum***	12
Erigeron ochroleucus	53	***Erysimum inconspicuum***	87
Erysimum asperum	9	***Gaillardia aristata***	58
Gaillardia aristata	102	***Gaura coccinea***	366
Gaura coccinea	189	***Grindelia squarrosa***	39
Grindelia squarrosa	57	***Gutierrezia sarothrae***	161
Gutierrezia sarothrae	482	***Helianthella uniflora***	1
Haplopappus acaulis	24	***Helianthus annuus***	26
Helianthus annuus	130	***Heterotheca villosa***	1729
Heterotheca villosa	2176	***Hymenoxys richardsonii***	59
Lactuca pulchella	87	***Lactuca pulchella***	90
Lactuca serriola	214	***Lactuca serriola***	119
Liatris punctata	761	***Liatris punctata***	208

Appendix A, Table 1 Continued

Linum lewisii	771	***Linum lewisii***	887
Linum rigidum	32	***Lygodesmia juncea***	165
Lygodesmia juncea	289	***Machaeranthera pinnatifida***	105
Medicago sativa	437	***Medicago sativa***	4311
Melilotus officinalis	3001	***Melilotus officinalis***	388
Opuntia polyacantha	70	***Opuntia polyacantha***	19
Pediomelum argophyllum	766	***Pediomelum argophyllum***	1764
Penstemon albidus	43	***Potentilla pensylvanica***	2
Phlox hoodii	65	***Ratibida columnifera***	695
Potentilla pensylvanica	15	***Rosa arkansana***	425
Ratibida columnifera	293	***Senecio canus***	12
Rosa arkansana	134	***Sisymbrium altissimum***	140
Senecio canus	11	***Solidago missouriensis***	85
Sisymbrium altissimum	168	***Solidago mollis***	864
Solidago missouriensis	90	***Sphaeralcea coccinea***	265
Solidago mollis	624	***Symphoricarpos albus***	385
Solidago simplex	6	***Symphyotrichum falcatum***	1
Sphaeralcea coccinea	42	***Taraxacum officinale***	388
Symphoricarpos albus	105	***Tragopogon dubius***	1158
Taraxacum officinale	2	***Vicia americana***	1581
Thermopsis rhombifolia	5	***Xanthisma spinulosum***	35
Tragopogon dubius	1520	***Zigadenus venenosus***	174
Vicia americana	689		
Xanthisma spinulosum	305		
Zigadenus venenosus	384		

Appendix A, Table 2. Species ranking within the 10 most abundant species by month during 2019 and 2020 sampling years.

2019				
Species	**Jun**	**Jul**	**Aug**	**Sep**
Achillea millefolium	x	x		
Artemisia cana				x
Aster falcatus			x	x
Astragalus gracilis	x			
Campanula rotundifolia		x		
Cerastium arvense	x			
Dalea purpurea		x		
Gaura coccinea	x			
Gutierrezia sarothrae			x	x
Helianthus annuus			x	
Heterotheca villosa		x	x	x
Lactuca serriola			x	
Liatris punctata			x	
Linum lewisii	x	x		
Lygodesmia juncea			x	x
Medicago sativa		x		
Melilotus officinalis	x	x	x	x
Pediomelum argophyllum		x		
Phlox hoodii	x			
Ratibida columnifera		x		
Sisymbrium altissimum		x		
Solidago missouriensis				x
Solidago mollis			x	x
Solidago simplex				x
Tragopogon dubius	x			
Vicia americana	x			
Xanthisma spinulosum			x	x
Zigadenus venenosus	x			
2020				
Achillea millefolium	x	x		

Appendix A, Table 2 Continued

Artemisia cana			x	x
Aster falcatus				x
Cerastium arvense	x			
Dalea purpurea		x		
Gaura coccinea	x			
Grindelia squarrosa			x	
Gutierrezia sarothrae			x	x
Helianthus annuus				x
Heterotheca villosa		x	x	x
Lactuca serriola			x	
Liatris punctata			x	
Linum lewisii	x			
Lygodesmia juncea			x	x
Machaeranthera pinnatifida				x
Medicago sativa		x		
Melilotus officinalis		x		
Pediomelum argophyllum		x		
Ratibida columnifera		x		
Rosa arkansana	x			
Sisymbrium altissimum	x			
Solidago missouriensis			x	x
Solidago mollis			x	x
Sphaeralcea coccinea	x			
Symphoricarpos albus		x		
Taraxacum officinale		x		
Tragopogon dubius	x	x		
Vicia americana	x			
Xanthisma spinulosum			x	
Zigadenus venenosus	x			

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APPENDIX B

INITIAL ASSESSMENT FOR COWPEA SUITABILITY AS A COVER CROP IN MONTANA

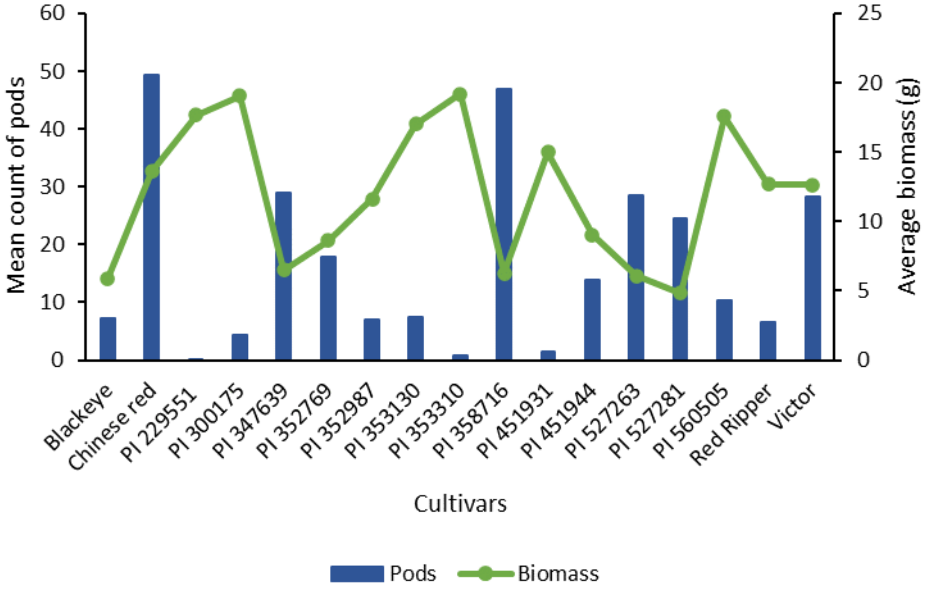
Dryland wheat production has been a common practice in the Canadian Prairies and the Great Plains of North America. In Montana, an alternative to conserve water and restore organic matter is the alternation between wheat and fallow (Morrill et al., 2001). More recently, there has been an increase in Montana farmers interested in using pulse and cover crops instead of fallow in this wheat production system (Long et al., 2014a; Long et al., 2014b; Miller et al., 2006). The use of cover crops improves the soil, reduces pest pressure, increases yield (Bullock, 1992; Kirkegaard et al., 2008; Miller et al., 2002), and offers nectar to beneficial insects (Tillman et al., 2012). Fischer (2009) reported that pulse and cover crops planted adjacent to wheat fields in Montana often increase abundance of the parasitoids *Bracon cephi* and *B. lissogaster*. As a likely consequence, stem lodging by wheat stem sawfly is reduced (Fischer, 2019). Some cover crops possess extrafloral nectaries, a food source easily accessed by beneficial insects (Gilbert and Jervis, 1998), as is the case for cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae: Papilionoideae) (Kuo and Pate, 1985; Pate et al., 1985). Cowpea is reported to benefit entomofauna (Fohouo et al., 2009), in addition to protect and enrich the soil (Clark, 2012; Crews and Peoples, 2005) and suppress weeds (Mhlanga et al., 2016).

Hence, we conducted initial tests to assess the suitability of this cover crop in Montana. We conducted greenhouse and field trials with 17 different cowpea cultivars, including commercial lines donated by Kamprath Seed, Inc. (Manteca, California, USA): “Victor”, “Red ripper”, “Chinese red”, and “Blackeye pea”, and 13 non-commercial landraces (Appendix B, Table 1). Cowpea plants were evaluated for flower production, extrafloral nectar production, pod and seed production, and biomass. The greenhouse experiments followed the methodology described in “Chapter 3”, while field trials took place at the MSU Western Agricultural Research Center, Corvallis, Montana, USA. Trials were conducted in a 120 m^2 area, with a total length of 2.74 m for each plot. There were four complete randomized design blocks to control for plants position at the greenhouse, where each plot received 24 seeds in a single row and the spacing within row was 10 cm. The end of each plot was marked using fava beans (*Vicia faba*) planted 15 cm apart from each other in the respective row. Because of a limited number of seeds for “PI 353310”, only 12 seeds of this race were planted in each row. A single plot was planted for “PI 229551” to increase our seed bank. The plots with lower availability of seeds were filled with other legumes, such as fava beans, chickling vetch (*Lathyrus sativus*), and winter pea (*Pisum sativum*). The planting procedure followed Quinn and Myers (2002), where 0.5 mL of Cruiser Maxx Vibrance Pulses were diluted in 9 ml of water to treat seeds, and 0.5 ml of this solution was used to individually treat seed lots. After air drying, the seeds were inoculated with Type I-Bradyrhizobium. All seeds were kept in a refrigerator until they were planted by hand approximately 3 cm in depth on May-13-2020. Weed management was conducted by using Prowl H20, followed by a biweekly hand weeding for 6 to 7 weeks.

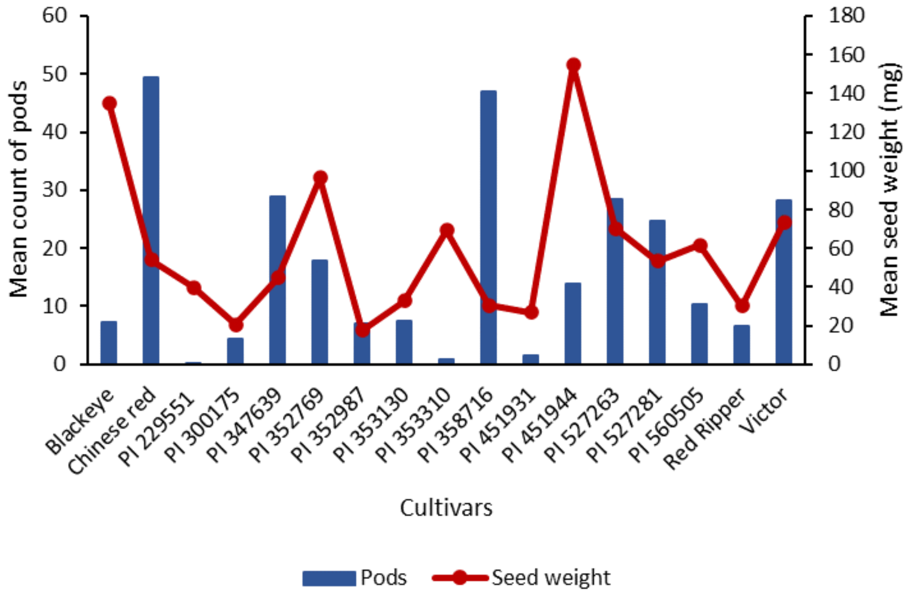
During the field trials in 2020, 23% of the plots had low or no emergence. Interestingly, these plots were mostly located in the northern third of the trials, where a rockier soil is found. Due to randomization, the races “PI 353130”, “PI 352769”, “PI 347639”, and “PI 352987” were mostly planted in the affected areas, and thus, results might not represent their true performance. This observed seed and seedling mortality could be due to fusarium root rot and *Aphanomyces* root rots, confirmed by MSU diagnostic lab. The number of pods produced per plants varied, with an average of 4 pods per plant. Some cultivars produced more than 10 pods per plant, and 50% of the cultivars produced more than 4 pods per plant (Appendix B, Table 2). The line “PI 353130” had similar pods per plant to “PI 451944” and “Chinese red”. However, “PI 353130” produced smaller pods and fewer mature seeds. Meanwhile, “Blackeye pea” had larger pods and seeds (Appendix B, Table 2). The cultivars with highest pods production were: “PI 347639”, “PI 527281”, “PI 527263”, “PI 358716”, and “Blackeye pea”. The number of seeds being produced followed the same pattern as pods per plant, and 7 cultivars produced relatively large yields (>500 kg/ha). The top 5 cultivars in yield were: “PI 527263”, “PI 527281”, “Blackeye pea”, “PI 358716”, and “PI 347639” (Appendix B, Table 2). Field trials were also conducted in 2021, where we again had 4 plots and a total of 56 plants. The cowpea cultivars “Blackeye pea”, “Chinese red”, “PI 451944”, “PI 527281”, “PI 347639”, “PI 527263” and “PI 358716” were sown on June 02 and on June 16. Weed management was conducted by using Glystar Plus at 3quarts/acre, Dual Magnum at 1pint/acre and Pemex at 3oz/acre. Cultivars planted earlier displayed higher yields (Appendix B, Table 4). We also noticed that production of flowers changed based on the sowing dates, interestingly, plants sown later had flowers earlier. When comparing yield for the different years, we noticed that “Blackeye pea” consistently had high yields, while “Chinese red” displayed lower yields in both years. “PI 527263” and “PI 527281” had high yields in 2020, but low yields in 2021. This result could be due to a higher sensitivity of these cultivars performance based on sowing time, because cultivars were planted early May in 2020, but early June in 2021 (Appendix B, Table 4).

During the greenhouse experiments, some of the cultivars did not produce pods during fall of 2018 (“Red ripper”, “PI 451931”, “PI 352987”, “PI 229551”, “PI 300175”), and 2019 (“PI 229551”, “PI 353130”, “PI 353310”, “PI 451931”, and “PI 560505”). However, when grown during Spring of 2019, all sown cultivars produced pods and seeds. Comparing this result with the field trials, we do not notice a pattern, and thus these observations might be due a casual response to a difference in soil type, occurrence of diseases, or growth time and period. Our greenhouse trials showed that the best yields were scored by “PI 527281”, “PI 358716”, “Chinese red”, “PI 527263”, and “Victor” (Appendix B, Table 3), which was similar to the field trials, with the exception of the commercial lines. Cultivars with greater biomass tend to have smaller yields (Appendix B, Fig. 1), and plants producing more pods have smaller seeds (Appendix B, Fig. 2). We also noticed that cowpea plants start to display inflorescence 5 to 9 weeks after sowing, where we can find mature pods 2 to 3 weeks later. New leaves were producing extrafloral nectar as soon as it sprouted, and extrafloral nectar was detectable in both IS-EFN and LS-EFN (Appendix B, Fig. 3).

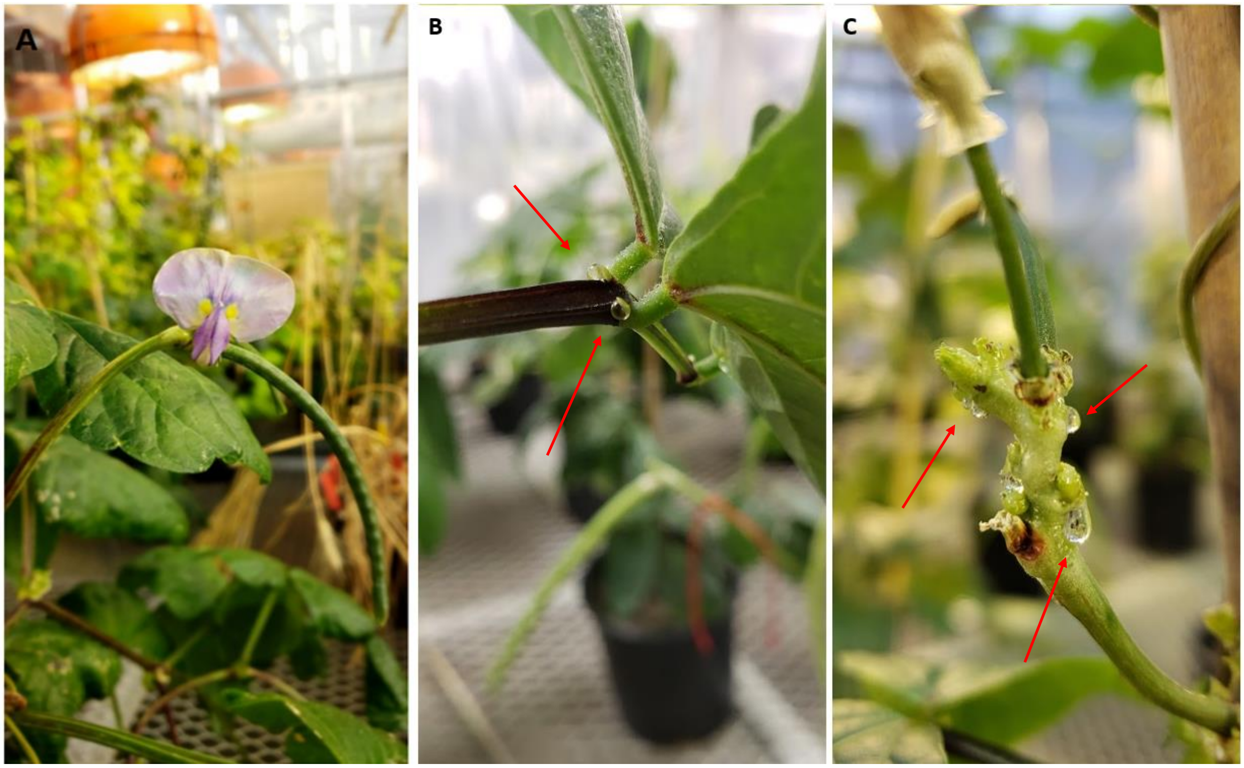
Knowing that floral vegetation can provide sugar resources that are important for parasitoid survival and can improve their efficiency as biological control agents (Heimpel and Jervis, 2005; Russell, 2015), flower nectar is an important resource in conservation biological control (Munir et al., 2018). Based on the information collected in initial trials, we were able to select cowpea cultivars to conduct the experiments detailed on “Chapter 3” to better explore the benefits of cowpea as a potential food source for *B. cephi* and *B. lissogaster*.



Appendix B, Fig. 1. Mean production of pods and biomass (grams) for the 17 tested cowpea cultivars during fall of 2018, spring of 2019 and fall of 2019.



Appendix B, Fig. 2. Mean production of pods and related average weight of seeds (mg) for the 17 tested cowpea cultivars during fall of 2018, spring of 2019 and fall of 2019.



Appendix B, Fig. 3. Cowpea inflorescence and green pod (A), and extrafloral nectar observed on the stipel extrafloral nectary (B) and the inflorescence stalk extrafloral nectary (C).

Appendix B, Table 1. Non-commercial pure line cultivars of cowpea used during experiments

Cultivar	Origin	Plant habit	Elevation (m)	Annual Precipitation (mm)
PI 358716	Ethiopia - Gedo	Erect	2498	91
PI 560505	Turkey - Çukurca	Semi-prostrate	1285	51
PI 451944	Mexico - Zacatecas	-	2488	80
PI 527263	Zimbabwe - Mashonaland Central	Erect	1261	121
PI 352769	Brazil - Ceara	Erect	187	65
PI 451931	Bolivia - Cochabamba	-	2551	36
PI 352987	India - Katrain, Kullu Valley	Erect	1279	216
PI 347639	Ethiopia - Gamo Gofa	Erect	1447	91
PI 353130	India - Bagar	Erect	2252	109
PI 353310	India - Mantholi	Erect	2050	100
PI 229551	Iran - Maragheh	Erect	1910	26
PI 300175	Palestine - Bethlehem	Erect	755	16
PI 527281	Zimbabwe - Filabusi	Erect	1080	58

Appendix B, Table 2. Performance of the different cowpea cultivars during field trials in 2020.

Cultivar	Plots planted	Plots producing seed	Pods/Plant	Seed weight (mg)
PI 347639	4	2	16.6	79
PI 527281	4	4	10.2	73.7
PI 527263	4	4	9.8	93.3
PI 358716	4	2	8.7	59
Blackeye pea	4	4	6	211.3
Chinese red	4	4	5.8	90
PI 451944	4	4	4.7	155.7
PI 353130	4	3	4.1	na
PI 352987	4	2	1.8	na
PI 300175	4	1	1.6	na
Victor	4	2	1.5	na
PI 353310	4	4	0.8	na
PI 352769	4	1	0.7	na
Red ripper	4	1	0.1	na
PI 451931	4	1	0.1	na
PI 560505	4	0	0	na
PI 229551	1	0	0	na

Appendix B, Table 3. Average performance of the 17 tested cowpea cultivars tested during greenhouse trials during fall of 2018, spring of 2019, and fall of 2019.

Cultivar	**Pods/plant**	**Seeds produced**	**Seed weight (mg)**
Blackeye pea	7	30	135.0
Chinese red	49	344	54.1
PI 229551	0	1	39.7
PI 300175	4	47	20.6
PI 347639	29	236	44.8
PI 352769	18	175	96.4
PI 352987	7	77	17.7
PI 353130	8	45	32.8
PI 353310	1	7	69.2
PI 358716	47	409	30.5
PI 451931	1	12	26.7
PI 451944	14	50	154.7
PI 527263	29	313	70.3
PI 527281	25	289	53.3
PI 560505	10	49	61.5
Red ripper	7	52	30.2
Victor	28	316	73.5

Appendix B, Table 4. Yield (kg/ha) for cowpea cultivars during field trials in both 2020 and 2021. In, 2021 seeds were sown on June 02 and June 16.

Yield (kg/ha)			
	2020	**2021**	
		June 02	**June 16**
PI 347639	1050.24	1129.49	484.61
PI 527281	1586.00	764.98	167.41
PI 527263	1863.98	612.51	220.70
PI 358716	1288.98	1020.83	510.65
Blackeye pea	1331.57	1662.84	390.05
Chinese red	634.40	350.73	6.82
PI 451944	624.31	825.20	258.64

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