

THE POTENTIAL OF SUGAR RESOURCES IN THE REPRODUCTIVE BIOLOGY
OF WHEAT STEM SAWFLY PARASITIDS

by

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DEDICATION

To my mom Nielze Silva Andrade, dad Joel dos Reis and brother Erick Andrade dos Reis whose trust and unconditional love always encourage me to pursue my dreams, no matter how far from home they keep taking me.

Para a minha mãe Nielze Silva Andrade, meu pai Joel dos Reis e meu irmão Erick Andrade dos Reis de quem a confiança e o amor incondicional sempre me encoraja a seguir os meus sonhos, não importa o quão longe de casa eles continuam me levando.

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ABSTRACT

The wheat stem sawfly, *Cephus cinctus*, is the most destructive insect pest of wheat, *Triticum aestivum*, in the Northern Great Plains of North America. Biological control by *Bracon cephi* and *Bracon lissogaster* is an important tool for integrated pest management of this pest, but parasitism rates are difficult to predict. Therefore, the main objective of this research was to characterize aspects of the reproductive biology of both parasitoid species to provide information that could enhance their effectiveness in biological control of *C. cinctus*. First, we investigated the role of diapause and the effects of sucrose feeding on reproduction of females. For that, we provided sucrose solution to overwintering and summer generation adult females, and we quantified and compared their longevity, egg load and egg volume. Our results showed no differences between overwintering and summer individuals of *B. cephi* and *B. lissogaster*. In contrast, sucrose feeding, increased longevity and egg load of both species and generations. The egg load of *B. cephi* was surprisingly low compared to *B. lissogaster*. However, only *B. cephi* increased egg volume when sucrose was provided. Our findings highlighted the contrasting life histories of both species, and showed the potential of sugar resources in enhancing their reproductive capacity. Subsequently, we investigated the effect of flower nectar on the same, above mentioned, reproductive traits of parasitoids. We chose buckwheat (*Fagopyrum esculentum*), lacy phacelia (*Phacelia tanacetifolia*), deerhorn clarkia (*Clarkia pulchella*), canola (*Brassica napus*), and safflower (*Carthamus tinctorius*) based on their occurrence as native plants, use in pollinator enhancement, and occurrence in rotational or cover crop plantings in Montana. We found that only *B. cephi* females benefitted from these flowering plants. The longevity and egg volume of females increased with buckwheat, and egg volume increased with both buckwheat and the native species, deerhorn clarkia. The strong effect of buckwheat on reproduction of *B. cephi* females suggests that flowers with similar nectar quality might have similar impacts. This information will be of great importance for selection of suitable flower species to enhance reproductive capacity of parasitoids through habitat management. Collectively, this research showed that there is potential to enhance effectiveness of parasitoids with sugar supplementation.

CHAPTER ONE

LITERATURE REVIEW

The Wheat Stem Sawfly, *Cephus cinctus* Norton, as a Pest of Wheat

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) (WSS) was first reported damaging wheat, *Triticum aestivum* L., in 1895, in the province of Manitoba in Canada (Wallace and McNeal 1966). Currently, the WSS is a major pest of wheat in the Northern Great Plains of North America (Beres et al. 2011). Originally, WSS preferred wild native grasses (Criddle 1923). Early records indicate that WSS occurred in common grasses of the genera *Agropyron*, *Bromus*, *Calamagrostis*, *Calamovilfa*, *Deschampsia*, *Elymus*, *Elyhordeum*, *Festuca*, *Hesperostipa*, *Hordeum*, *Koeleria*, *Nassella*, *Phleum*, *Poa*, *Pseudoroegneria*, *Stipa*, *Thinopyrum* and *Thinopyrum* (Ainslie 1920, Wallace and McNeal 1966, Cockrell et al. 2017). After widespread planting of wheat began on homesteads, the host range of WSS increased to include spring wheat within ten years after cultivation began (Ainslie 1920).

Historically, WSS damage had been reported only in spring wheat, while winter wheat escaped damage because of early maturation (Davis 1948, Wallace and McNeal 1966). Due to a decrease in acreage of spring wheat from 1921 to 1945, host availability was reduced, and by 1980, widespread losses due to WSS occurred in winter wheat grown in Montana (Morrill 1983). The pest adapted to winter wheat by emerging 20 days earlier than in previous records, thus synchronizing oviposition activity with susceptible growth stages of winter wheat (Morrill and Kushnak 1996).

The WSS is widely distributed in North America, east to west from Pennsylvania and Georgia to the Pacific Ocean, and north to south from the province of Alberta in Canada to the state of Texas in the United States (Wallace and McNeal 1966, Smith 1979, Ivie 2001). Economically important damage has been primarily reported in the northern Great Plains of Alberta, Saskatchewan, Manitoba, North and South Dakota, Montana, and Wyoming (Ainslie 1929, Painter 1953, Wallace and McNeal 1966, Weiss et al. 1992). More recently, damage caused by WSS has expanded southward, into southeastern Wyoming, the Nebraska Panhandle, and northeastern Colorado (Irell and Peairs 2011, Lestina et al. 2016). Annual foregone revenue associated with WSS damage and management in wheat has been reported to exceed \$80 million in Montana alone (Bekkerman 2014).

The Wheat Stem Sawfly

Biology

The WSS is univoltine. In Montana, adult emergence begins in late May or early June and lasts three to four weeks, but timing of emergence is influenced by temperature and latitude (Wallace and McNeal 1966, Weiss and Morrill 1992, Perez-Mendoza and Weaver 2006). Males typically emerge before females (Holmes 1979) and adults live five to eight days, depending on environmental conditions, and during the adult stage they are not known to feed (Wallace and McNeal 1966). Copulation occurs immediately after emergence and reproduction is arrhenotokous (Smith 1938, Mackay 1956), with fertilized

eggs producing diploid females, and unfertilized eggs producing haploid males (Wallace and McNeal 1966).

Adult activity is associated with sunny conditions, when temperatures range from 17 to 32°C and wind speeds are minimal (Ainslie 1929, Seamans 1945). Both males and females are weak fliers because limited flight distances are required to find suitable hosts (Sing 2002). Oviposition begins a few days after emergence and females prefer to oviposit in succulent, elongating and large diameter stems (Zadoks 31-34) (Holmes and Peterson 1960, Zadoks et al. 1974). The female deposits a single egg in the stem per visit, but multiple individuals may be found in stems because subsequent females are unaware of earlier oviposition or feeding larvae (Criddle 1923, Buteler et al. 2009). Adult females can produce as many as 50 eggs of equal size and maturity (Ainslie 1920).

Eggs hatch in approximately 7 days and the larva starts to feed on parenchymal and vascular tissues of the stem (Ainslie 1920). The larvae are cannibalistic (Wallace and McNeal 1966, Buteler et al. 2009, 2015) and when more than one egg is deposited in the stem, only one larva will survive. There are four to five larval instars and completion of larval development usually coincides with plant senescence and the duration of this period depends on the host plant phenology (Holmes 1954). When mature, the larva seeks the extreme base of the stem in response to visible cues of infrared light penetrating the stem wall and decreasing moisture content in the stem (Davis 1955, Holmes 1979). At the base of the stem, the larva prepares its hibernaculum by cutting a V-shaped groove entirely around and inside the stem, usually at or slightly above ground level (Ainslie 1929). This groove weakens the stem so that it breaks and lodges, especially in windy or

rainy conditions. The remaining part of the stem forms a “stub” that serves as an overwintering chamber for the larva (Munro 1947). The following spring the larva pupates, completes metamorphosis, and an adult emerges (Munro 1945).

Damage

Adult female WSS insert their saw-like ovipositor into the stem and insert an egg (Ainslie 1929). This behavior causes limited damage in the stem and is unlikely to produce an avenue for diseases (Wallace and McNeal 1966). Stem damage begins as soon as the larva emerges from the egg and starts to feed by boring up and down inside the stem. While feeding, the developing larva consumes the parenchymal tissue and vascular bundles of the plant, causing reductions in photosynthetic capacity (Macedo et al. 2005). The larval feeding injury also reduces size, weight and number of kernels in an individual head (Munro et al. 1947, Morrill et al. 1992). Reduction in head weight due to larval feeding is between 3 and 30% (Holmes 1977, Morrill et al. 1992, Özberk et al. 2005, Delaney et al. 2010). Subsequent damage occurs when the larva cuts the V-shaped groove in the stem wall. After girdling of the interior, the stem easily breaks and lodges on the ground. Many of the fallen heads are lost during harvest, and the heads on the ground, together with wet weather conditions, favors molding or germination of the seeds (Wallace and McNeal 1966). These volunteer germinated wheat plants can host pathogens and/or arthropod pests as well as compete for soil nutrients and water between the harvest of one crop and the emergence of the next one (Cook and Veseth 1991).

Management

Management practices to control WSS include biological control, chemical control, host-plant resistance, and cultural control. Currently, no single control method has effectively controlled WSS populations (Morrill et al. 2001), therefore a comprehensive integrated pest management program is needed (Beres et al. 2011).

Cultural Control. Since the early 1900s, cultural practices have been recommended to control WSS. Early recommendations included burning, deep plowing, early harvesting, and destruction of host plant reservoirs (Beres et al. 2011). However, most of those practices were shown to be inefficient, impractical, or harmful to the soil and/or natural enemies. Recently, trap crops, crop rotation, and delayed planting have been used and showed promising results (Seamans 1928, Morrill and Kushnak 1999, Morrill et al. 2001, Shelton and Badenes-Perez 2006, Beres et al. 2011).

Chemical Control. The use of insecticides has been a challenge to control WSS because of its short flight period, prolonged adult emergence interval and cryptic life cycle (Beres et al. 2011). Many systemic and contact insecticides have been tested, but they had no significant effect on population survivorship. In the 1960s, satisfactory results were obtained using heptachlor (a non-systemic stomach and contact organochlorine insecticide) with wheat seeds (Holmes and Peterson 1963). However, with this insecticide, considerable mortality only occurred for early instars in the lower internodes of the stem where insecticide was more concentrated (Holmes and Peterson 1963). Heptachlor has also been banned in the US since 1988 because of its persistence in

the soil (Anonymous 1997). More recently, the Montana Department of Agriculture has issued a special local need pesticide registration for phorate (Thimet[®]20-G) an organophosphate soil and systemic insecticide to control WSS larva. Recent data have shown that the use of Thimet[®]20-G caused 64-100% reduction of stem cutting (Montana Department of Agriculture 2015). However, due to its high toxicity to fish, birds, and mammals, Thimet[®]20-G cannot be applied more than once per crop per season, and it must be incorporated into the soil and applied 85 days before harvest (Montana Department of Agriculture 2015).

Host Plant Resistance. Stem solidness in wheat is the most common type of host resistance mechanism used against the WSS. Farstad (1940) was the first to relate stem solidness with WSS resistance: pith expression in the lumen of the wheat stem reduces larval survival. By late 1940s, the first solid-stemmed cultivar named ‘Rescue’ was developed and quickly became widely grown in WSS-affected areas of North America (Platt et al. 1948). After that, many solid and semi-solid stemmed varieties were developed. Solid-stemmed cultivars are widely used because of their efficiency in WSS control, but this resistance mechanism is not always reliable because solidness is influenced by photoperiod and light intensity during stem elongation (Beres et al. 2011, 2017). Pith development can be inhibited by shady and cloudy conditions (Eckroth and McNeal 1953, Holmes 1984). Furthermore, in the absence of WSS, solid-stemmed cultivars yield less than hollow-stemmed cultivars (Shanower 2008).

Host-plant attractiveness is another plant resistance mechanism to WSS. Non-attractive plants can provide a level of resistance. Weaver et al. (2009) showed that

ovipositing females overwhelmingly preferred cultivars with greater amounts of an attractant volatile compound. Thus, the cultivars that release less of the plant volatile are likely to be less infested.

Further, plant volatiles might also be used to attract parasitoids of WSS. Peck (2004) showed that high infestation of WSS can alter the volatile production of wheat plants. Some synthetic volatiles, matching those produced by WSS-infested plants, generate attractive responses from *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae) (Perez 2009).

Biological Control of Parasitoids. A total of 10 parasitoid species have been reported to parasitize WSS in native and feral grasses (Criddle 1923, Marsh 1979, Morrill 1997), but only two species, *B. cephi* and *B. lissogaster*, are known to commonly parasitize larvae in wheat stems (Davis et al. 1955, Somsen and Luginbill 1956, Morrill et al. 1994). Slow adaptation of parasitoids to wheat may be due to lack of synchrony between parasitoids and their hosts. Parasitism occurs during the wheat growing season when the WSS larva is feeding on the host plant (Holmes et al. 1963). However, wheat maturation is more rapid than most feral grasses, and when the wheat stem ripens, the WSS larvae descend to the base of the plant, cut the stems and prepare hibernaculae where they will overwinter (Davis 1955, Holmes 1979). At this point, large WSS larvae are unlikely to be parasitized. Therefore, adaptation of parasitoids to wheat depends on how fast they can reproduce and develop to synchronize with WSS larval stage and wheat phenology (Holmes et al. 1963).

Bracon cephi and *B. lissogaster* are sympatric specialist ectoparasitoids with similar life histories and phenologies (Runyon et al. 2001). *Bracon cephi* is solitary (only one egg is laid per host), and *B. lissogaster* can be either solitary or gregarious (more than one egg is laid per host) (Nelson and Farstad 1953, Somsen and Luginbill 1956). Both species have two generations per year (bivoltine), unless the growing season is too short due to drought or excessive heat causing early maturity of wheat (Holmes et al. 1963). Parasitism by *B. cephi* and *B. lissogaster* have two positive impacts on wheat crops, first indirectly by killing the larva and thus reducing future damage in subsequent crops, and second by immediately reducing yield loss due to paralysis of the larva ceasing its feeding (Buteler et al. 2008, Bekkerman 2014). In a recent study, Buteler et al. (2015), showed that, in Montana, parasitism is one of the most important causes of larval mortality. Parasitism killed up to 34% of larvae and 12% of this mortality was irreplaceable; that is, the mortality caused by *B. cephi* or *B. lissogaster* could not be replaced by another mortality factor (Buteler et al. 2015).

Attempts at introducing other biological control agents have been unsuccessful. Release of *Collyria calcitrator* (Gravenhorst) (Hymenoptera: Ichneumonidae), a parasitoid of European wheat stem sawfly, *Cephus pygmaeus* L. (Cephididae), was first undertaken in early 1950s in Montana and North Dakota, but it did not become established (Davis 1955). Later on, *Collyria coxator* (Villers) (Ichneumonidae) and *Bracon terebella* (Braconidae), also parasitoids of *C. pygmaeus*, were released, but they also failed to establish due to specific adaptation of these parasitoids to the European sawfly species (Smith 1931). More recently, *Collyria catoptron* (Wahl) (Ichneumonidae),

a parasitoid of *Cephus fumipennis* (Cepidae) was introduced from China for quarantine evaluation of its capacity to control WSS (Rand et al. 2016). Due to host incompatibility, this species is unlikely to be a suitable agent for biological control of WSS (Rand et al. 2016).

Bracon cephi (Gahan) and *Bracon lissogaster* Muesebeck

Biology

Bracon cephi. *Bracon cephi* has two generations per year (Criddle 1923, Nelson and Farstad 1953, Morrill 1997). However, the success of the second generation depends on host plant phenology, and how late in the season the first generation females continue to oviposit. Eggs deposited by first generation parasitoid females in June or July will hatch, feed on the larval host, pupate, and emerge as second generation adults, whereas the progeny of eggs laid in July or August overwinter as larvae (Holmes et al. 1963). The first generation has a synchronized emergence with WSS, but parasitoids do not start to oviposit right away. There is a pre-oviposition period of 12 to 21 days (Nelson and Farstad 1953, Holmes et al. 1963). The reason why this pre-oviposition period is needed is unknown, however, speculation have been made on whether this delay is required to restore nutrient reserves after overwinter, to allow parasitoid females mature their eggs (Nelson and Farstad 1953) or for WSS larvae to develop sufficiently to permit larval parasitoid development (Holmes et al. 1963). In contrast, second generation females start to oviposit almost immediately after emergence (Holmes et al. 1963).

Newly emerged *B. cephi* and *B. lissogaster* adults exit by chewing a hole through the walls of cocoon and stem, escaping directly from the cocoon to the exterior (Nelson and Farstad 1953). Males typically emerge first, but females always outlive males. Early records reported that adult males live from 10 to 14 days, and females live as long as four weeks (Nelson and Farstad 1953).

Parasitoid activity, especially oviposition, is more pronounced on sunny days after a shower (Nelson and Farstad 1953). Adults have been observed foraging for food and consuming droplet moisture present on leaves or nectar of flowers along headlands and roadsides (Nelson and Farstad 1953). To locate the host, it is likely that *B. cephi* uses WSS-infested wheat plant volatiles to find the infested stem (Perez 2009) and vibrations or sounds produced by WSS larva within the stem (Mankin et al. 2004). Females can deposit two to four eggs daily, and have six to ten mature eggs in the ovaries (Nelson and Farstad 1953).

Once the host has been located, the female inserts her ovipositor through the stem wall and inserts a toxin that paralyzes the host larva before egg deposition (Clausen 1940). Typically only one egg is deposited per host, and the egg is not attached to, and not necessarily laid on, the host (Holmes et al. 1963). The larva hatches in 1 to 2 days, locates the host, attaches itself with its mandibles and immediately starts feeding (Nelson and Farstad 1953). Development is completed in approximately 10 days; typically the host is fully consumed except for the integument (Nelson and Farstad 1953). The mature larva spins a cylindrical cocoon that is firmly held lengthwise to the inside of the stem (Nelson and Farstad 1953). Cocoons of the first generation are often loosely woven,

whereas cocoons of the second generation are tightly woven (Nelson and Farstad 1953). Most *B. cephi* larvae overwinter above ground in standing stems. Unlike WSS larvae that overwinters below the soil surface, *B. cephi* is exposed to unfavorable winter conditions (Holmes et al. 1963). Therefore, the ability to withstand the low temperatures is critical for survival. *Bracon cephi* survives by producing solutes, primarily glycerol, that depresses the melting points of the hemolymph greatly and even allow survival if frozen (Salt 1959). Larvae pupate and adults emerge the following June.

Bracon lissogaster. *Bracon lissogaster* and *B. cephi* have similar biology, but, *B. lissogaster* more readily completes the second generation and it has a shorter pre-oviposition period of 6 to 8 days (Somsen and Luginbill 1956). Because of its gregarious behavior, one to four eggs can be found per host (Somsen and Luginbill 1956). Larval development is completed in 6 to 8 days, but when more than two larvae are feeding upon the same host, the development time is reduced, most likely because of the decreased availability of food (Somsen and Luginbill 1956). Even under these crowded conditions, larvae develop normally and completely, but they are smaller than those that feed solitarily (Somsen and Luginbill 1956).

Causes of Variation of Body Size in Insects

Body size is a key life-history trait in insects that determines potential longevity and fecundity of females and consequently affects their reproductive success (Stearns 1992). Adult body size in holometabolous insects is determined genetically and modified by environmental conditions during larval development (Honek, 1993). Intraspecific

variation in body size often occurs as a consequence of latitudinal or altitudinal clines (reviewed in Mousseau 1997, Blackburn et al. 1999, Chown and Gaston 1999, 2010, Blanckenhorn and Demont 2004, Dillon et al. 2006). Bergmann's rule describes an ecogeographical pattern where organisms at higher latitudes or altitudes tend to be larger than organisms at lower ones (Bergmann 1847). Bergmann (1847) posits that heat loss of endotherms (warm-blooded) is proportional to their surface-to-volume ratio. As body size increases, body volume increases faster than body surface area, and therefore, with a lower body surface-to-volume ratio organisms can reduce heat loss. This rule has been shown to be true for endotherms, but the same pattern is also true for many ectotherms (cold-blooded), and particularly for insects (Ray 1960, Chown and Gaston 1999, 2010, Blanckenhorn and Demont 2004, Dillon et al. 2006).

Although many insect species follow Bergmann's rule, many other species show an opposite pattern, with body size decreasing as latitude or altitude increases. The converse of Bergmann's rule arises as a result of variation in season length (Masaki 1967, Roff 1980, Chown and Gaston 1999, 2010, Blanckenhorn and Demont 2004). At higher latitudes/altitudes, season length becomes shorter and time available for growth becomes a limiting factor for body size, because larger size can be attained by prolonging growth (Masaki 1967, 1972). To compensate seasonal limitations at higher latitudes or altitudes, individuals may evolve a faster growth rate compared to their lower latitude conspecifics (Levinton and Monahan 1983, Conover and Present 1990, Blanckenhorn and Demont 2004).

Length of season will also influence the number of generations per year (voltinism) (Roff 1983, Stearns 1992). In general, the length of time needed to complete a generation increases along with season length until a critical point is reached at which the season length supports an additional generation (Tauber et al. 1986). At this tipping point, an additional generation will be favored to maximize the intrinsic rate of natural increase of the population (r-strategy) (Fisher 1958). To accommodate more than one generation into a season, a decrease in growth time will be favored (Masaki 1972). Therefore, multivoltine species have to develop in a shorter time, which consequently affects the adult body size because both are positively correlated (Roff 1980).

Body size of adults will also depend on the quantity and quality of food consumed during larval feeding. For example, *B. cephi* and *B. lissogaster*, are idiobiont parasitoids that paralyze their host before oviposition (Nelson and Farstad 1953, Somsen and Luginbill 1956). As a consequence of paralysis, host feeding and growth stops and development of parasitoid offspring is restricted by the size of the host at the moment of oviposition (Godfray 1994). Nutrients acquired during larval feeding supports growth and development of the parasitoid larva, with accumulated nutrients allocated during metamorphosis into the adult body plan (Boggs and Freeman 2005). In solitary parasitoids, host size is one of the main parameters influencing offspring size (Godfray 1994). In gregarious parasitoids, the number of eggs laid per host (clutch size) can also influence the size of the offspring (Godfray 1994).

Insect Body Size and Fitness

In almost all organisms, a large variation in body size among individuals can be observed. How this variation in size can affect fitness is a question that has been addressed for many years in the literature on life history and behavioral ecology (Stearns 1992, Honek 1993, Godfray 1994, King and Lee 1994). This relationship can be especially important in parasitoids, because they accumulate resources and complete development in or on a discrete host and they do not grow after emergence (Godfray 1994, Visser 1994, Harvey et al. 1994, Mackauer et al. 1997, Harvey et al. 1999). Because the importance of the host to the immature parasitoid, the reproductive decisions made by the ovipositing female have a direct link to fitness (Godfray 1994). By assessing host size, host quality or even clutch size, the parasitoid female determines the offspring size and therefore their potential reproductive capacity (Godfray 1994). The size advantage hypothesis in parasitoids has been used since Charnov (1981) to explain male eggs being laid in small hosts and females in large hosts. It is assumed that female fitness shows a sharper increase with size than male fitness (Charnov 1981).

The relationship between body size and fitness has been studied extensively in parasitoid females. In the majority of those studies, fitness is measured in the laboratory by examining life history components such as fecundity or longevity and often both are positively correlated with size. For example, larger females have more eggs in the ovarioles, have larger eggs and live longer than small females (Charnov 1981, Charnov and Skinner 1984, O'Neill and Skinner 1990, Visser 1994). However, being large does not necessarily translate into a higher reproductive success in the field. If larger females

produce more eggs, but rarely get the chance to oviposit (i.e. low host density), a positive effect of body size on egg production is unlikely to affect realized fitness (Heimpel and Jervis 2005). Likewise, if predation is an important factor depressing survival in the field, the effect of body size in increasing longevity may be of small importance (Heimpel and Jervis 2005). The constraints acting on size, such as host density or predation, should also be accounted for when studying the relationship between size and fitness. Variation in fitness may well be attributed to other factors influenced by body size. However, these factors are often difficult to account because some may have additive effects upon fitness, while others may be counteracting (O'Neill and Skinner 1990). Few studies have tested the relationship between size and fitness in the field, and among these the results are quite ambiguous (Visser 1994, West et al. 1996, Ellers et al. 1998, Ellers and van Alphen 2001, Segoli and Rosenheim 2015). By comparing the results from the field and the laboratory experiments, Visser (1994) showed that fitness increases much more rapidly with increasing female size in the laboratory than under field conditions.

Diapause and Reproductive Success

A striking feature of the life-history of insects is their physiological and behavioral adaptation to seasonal environments. In most regions of the world, favorable conditions that are suitable for growth and reproduction generally prevail only during particular seasons. Therefore, to synchronize activities to favorable times and to enhance survival during unfavorable conditions, many species undergo a state of dormancy (Tauber et al. 1986, Leather et al. 1993).

Diapause is a genetically programmed dynamic state of dormancy, characterized by low metabolic activity (Tauber et al. 1986, Danks 1987) and is triggered by seasonal cues such as temperature or photoperiod (Danks 1987). Although diapause is necessary for surviving through adverse conditions, it can be very costly. First, the timing of diapause is critical. The induction and termination of diapause are associated with a complex series of physiological changes, and typically this decision cannot be reversed if the season extends beyond the expected period. Hence, a long diapause may cause a disruption in mating and oviposition opportunities (Neal et al. 1997). Second, diapause could have an adverse effect on survival rates. This can either be caused by the low temperatures to which the overwintering stages are exposed (Irwin and Lee 2000), by starvation due to depletion of stored energy reserves (Storey and Storey 1986, Hahn and Denlinger 2007) or by exposure to other mortality factors. For instance, individuals of *B. cephi* and *B. lissogaster* are at high risk of mortality because they overwinter above ground, in the upper parts of the wheat stems that are removed and processed during harvesting and threshing operations (Beres et al. 2011, Meers 2005).

Finally, diapause could impose an energetic cost on reproductive success of postdiapause individuals (Ishihara and Shimada 1995, Ellers and van Alphen 2002, Matsuo 2006, Hahn and Denlinger 2007, 2011, Larson and Duan 2016). Many of these effects can be attributed to the allocation of metabolic reserves during diapause. For example, overwintering larvae of *B. cephi* accumulate great concentrations of glycerol, equivalent to 25 % of their body mass, to prevent injury to the cells even if they freeze (Salt 1959). Thus, a substantial amount of energy reserves are required to support

synthesis of these protective molecules. As a result, the allocation of energy reserves towards diapause maintenance trades-off against the allocation of resources into postdiapause functions (Denlinger 1979, Danks 1987). This is especially important for parasitoids, because they accumulate resources in or on a discrete host, which usually is not much larger than the parasitoid itself (Godfray 1994, Jervis et al. 2008), and they have very limited or no access to food resources during diapause (Hahn and Denlinger 2011). Several studies have found that postdiapause females carry a smaller egg load (Ishihara and Shimada 1995, Ellers and van Alphen 2002, Larson and Duan 2016) and have decreased longevity (Larson and Duan 2016). In species with facultative diapause, non-diapause females have been found to have higher levels of lipid reserves (Fordyce et al. 2006), larger body size (Sadakiyo and Ishihara 2012), and increased egg fertility (Bradshaw et al. 1998) than postdiapause ones. In contrast, other studies showed no costs of diapause on postdiapause individuals (Peferoen et al. 1981, Jansson et al. 1989, Eijs and van Alphen 1999).

Ovarian Dynamics

Ovarian dynamics in insects describes the processes of egg maturation, oviposition and egg resorption and how they interplay each other (Richard and Casas 2012). At the individual level, factors such as physiological state and host availability determine the rate at which those processes will occur (Wheeler 1996, Papaj 2000, Nager 2006, Krysko et al. 2008). The most efficient rate of egg maturation will happen if a female insect allocates its resources to egg production and longevity in a way that it dies

immediately after laying the last egg on a suitable host. In this case, no waste of resources would occur by maturing an excess of eggs that are never laid, or in fueling longevity after eggs have been exhausted. However, in stochastic environments there is great variability in host availability, food availability, weather conditions and predation; therefore, it is impossible to predict a precise evolutionary match of eggs produced with realized reproductive opportunities at the individual level (Rosenheim 1996). Parasitoid females often die before getting the chance to lay all their eggs (time limited) (Lotka 1925, Nicholson and Bailey 1935, Hassell 1978, 2000, Murdoch et al. 2003). In this case, females should be capable of egg resorption to reallocate the resources from the excess of eggs that make no contribution to fitness to increase longevity (Rosenheim et al. 2000). In contrast, females that exhaust their entire complement of eggs while hosts are still available (egg limited), should increase egg maturation even if such strategy would impose an expense of longevity (Rosenheim 1996). Ovarian processes are therefore dynamic because they respond to environment stochasticity by balancing the flow of nutrients from soma to egg production and vice versa to improve individual reproductive success (Rosenheim 1996, 2011, Rosenheim et al. 2008).

The egg load, which is defined as the number of eggs that a female carries in a given moment in her lifetime (Jervis et al. 2005), is a function of the egg maturation strategy and it is also adjusted at the level of the individual (Papaj 2000). In the majority of parasitoid species, females eclose with few or no mature eggs in the ovaries, and egg maturation occurs throughout their adult life (Jervis et al. 2001). This egg maturation strategy, also called synovigeny (Flanders 1950), confers reproductive plasticity to

females that are able to mature eggs in response to variation in host availability (Ellers et al. 2000, Rosenheim et al. 2000, Ellers and Jervis 2003). Ovarian dynamics in such species is regulated through oogenesis (formation of follicles in the ovarioles, followed by yolk and chorion deposition in the oocytes), oviposition and oosorption (degeneration and resorption of yolked oocytes) (Bell and Bohm 1975, Ellers and van Alphen 1997, Papaj 2000). Less commonly, parasitoids emerge with their lifetime complement of eggs, already mature. This strategy is called pro-ovigeny (Flanders 1950), and such species have the advantage of maximizing the number of eggs laid early in the lifetime (Ellers et al. 2000, Rosenheim et al. 2000, Ellers and Jervis 2003). However, due to the fixed and limited amount of eggs in the ovaries, pro-ovigenic species may experience egg limitation after they exhaust their entire complement of eggs before death. Egg limitation has been considered the most fundamental constraint to reproductive success in pro-ovigenic species (Rosenheim et al. 2000).

Egg limitation could also be a reproductive constraint for synovigenic parasitoids. A transient egg limitation can occur when eggs supplies are exhausted and hosts are still abundant (Rosenheim et al. 2000, Rosenheim 2011). Even though insects can mature eggs relatively rapidly, the process does not occur instantaneously (Papaj 2000, Bodin et al. 2007, 2009, Casas et al. 2009). Moreover, some synovigenic females might have limited capacity to store matured eggs in the ovaries (Iwata 1964). Thus, even by having the capability to produce eggs throughout their lifetime, synovigenic species may experience transient egg limitation to await for further egg maturation before resuming reproduction (Charnov and Skinner 1984, Heimpel and Rosenheim 1998, Casas et al.

2000). Age is also an important factor influencing the rate of egg maturation in synovigenic females. As females age, degradation of ovarian function increases and egg maturation declines (Boggs 1997, Giron and Casas 2003). Synovigenic females therefore, can also experience permanent egg limitation just like pro-ovigenic (Rosenheim 1999). In both cases, pro-ovigenic and synovigenic populations that are subjected to losses in reproductive opportunity because of egg limitation are expected to evolve over a long time frame increasing fecundity or accelerating egg maturation (Rosenheim 1996, 2011, Sevenster et al. 1998).

Effects of Floral Resources and Sugar Feeding on Parasitoid Reproductive Success

Intensification of modern agriculture has resulted in a simplification of the landscape by expansion of the field size and removal of non-crop habitat (Bianchi et al. 2006). As land devoted to monoculture increases, landscape complexity decreases, culminating in oversimplified habitats and potentially contributing to an increase in herbivore densities (Matson et al. 1997, Bianchi et al. 2006, Veres et al. 2013). Such patterns may arise because natural enemies (predators and parasitoids) may be more abundant and/or efficient in reducing herbivore densities in more diverse plant habitats (Root 1973). Diverse vegetation can provide food resources to natural enemies, plus alternative hosts and shelter for adverse conditions (Landis et al. 2000, Tylianakis et al. 2004, Lavandero et al. 2005, Berndt et al. 2006, Simpson et al. 2011, Gurr et al. 2017). In particular, floral vegetation could provide adult parasitoids with sugar resources that are required in essential physiological processes, such as survival; thus plant diversity,

including floral vegetation, could enhance their efficiency as biological control agents (Heimpel and Jervis 2005). Floral resources should be integrated into the landscape in a way that is spatially and temporally favorable to parasitoids, not be suitable for pests, and also practical for producers to implement (Landis et al. 2000, Gurr et al. 2017, McCabe et al. 2017). In Montana, there is increasing interest in growing cover crops (Jones et al. 2016) and also flowering pulse crops in rotations (McVay et al. 2013). These crops are grown for profit as well as for protection and enrichment of the soil, which consequently can increase subsequent crop yield, reduce soil erosion, and reduce fertilizer and pesticide use (Crews and Peoples 2005). Furthermore, these crops can add diversity to the landscape, and potentially be a source of sugar to natural enemies (Bugg and Waddington 1994).

Feeding on sugar may benefit parasitoid reproductive success directly, by reducing the risk of egg limitation (Rosenheim et al. 2000) and increasing egg maturation rate (Heimpel et al. 1997, Olson and Andow 1998, Tylianakis et al. 2004, Zhang et al. 2011) and/or indirectly by increasing longevity and, consequently, reducing the risk of time limitation by providing extra time for foraging and oviposition (Giron et al. 2002, Berndt and Wratten 2005, Lee and Heimpel 2008, Géneau et al. 2012). In the field, parasitoids feed on flower nectar or honeydew to obtain sugar (Wäckers et al. 2008). A growing number of studies have shown that the presence of flowering plants can increase parasitoid abundance and parasitism levels (Stephens et al. 1998, Tylianakis et al. 2004, Lavandero et al. 2005, Berndt et al. 2006, Simpson et al. 2011). However, many other studies manipulating floral resources show inconsistent results in parasitism rates

(Cappuccino et al. 1999, Nicholls et al. 2000, Berndt et al. 2002, Lee and Heimpel 2005, Lee et al. 2006, Winkler et al. 2010). Recent models have shown that the provision of appropriate food resources to parasitoids only enhance biological control if prey refuge is reduced (Chakraborty et al. 2017). Similarly, Rand et al. (2014) conclude that the implications of habitat diversification at the landscape scale could play a role in suppressing agricultural pest populations via reductions in area of suitable crop hosts. Some studies have shown a counteracting effect in sugar consumption by parasitoids, i.e. reduced longevity (Ellers et al. 2011) and reduced host searching behavior (Lightle et al. 2010). One possible explanation for this counteracting effect on reproductive success is that parasitoids may not be limited by sugar resources in the field (Heimpel and Jervis 2005), or, possibly, parasitoid survival is mainly compromised by other factors, such as high predation, weather conditions, or cultural practices (Holmes et al. 1963, Runyon et al. 2002, Meers 2005). Moreover, not all floral resources are suitable for parasitoid use. Flower morphology is extremely important for plant-pollinator interactions (Wäckers et al. 1996, Patt et al. 1999, Vattala et al. 2006). A mismatch between flower morphology and parasitoid morphology might explain the lack of effect of flower resources in parasitism rates.

Large body size is often correlated with an increase in the amount of resources carried-over from larva feeding on the host (Spradberry and Sands 1981, Honek 1993, Ellers et al. 1998). Large individuals are known to store more energy reserves and to produce more eggs than smaller conspecifics (Bezemer et al. 2005). Thus, survival and egg production are dependent on the size of the female. Because of this relationship,

small females were shown to rely more heavily on sugar feeding for survival and reproduction (Rivero and West 2002, Bezemer et al. 2005). Sugar feeding may also be beneficial for synovigenic females. By feeding on carbohydrates, the rate of reserves uptake for survival is slowed down, and more of the reserves can be allocated into egg maturation (Casas et al. 2005, Jervis et al. 2008). In pro-ovigenic species, eggs are completely mature at emergence (Jervis et al. 2001), but sugar feeding can also be beneficial to increase dispersal capacity and longevity (Lee et al. 2006, Bianchi and Wackers 2008, Jervis et al. 2008).

Both species, *B. cephi* and *B. lissogaster*, are likely to consume sugars. Nelson and Farstad (1953) reported *B. cephi* adults foraging flowers and consuming nectar in the field. Whereas, Somsen and Luginbill (1956) reared adults of *B. lissogaster* with honey and sugar solution. Despite this, little is known about how sugar feeding can benefit these two species.

Research Objectives

Biological control is an important component of integrated pest management of WSS. Therefore, the main objective of this research was to provide detailed information on the life-history traits that influence reproductive success of *B. cephi* and *B. lissogaster*. This information is often required to develop effective biological control programs against agricultural pests. Thus, it may be of great value in biological control of WSS in Montana. To achieve this goal, in the first study, we quantified the longevity, egg load and egg volume of the sympatric specialists, *B. cephi* and *B. lissogaster* to test whether

these parameters differ among overwintering and summer generation adult females. We also investigated the effect of sucrose feeding on the quantitative expression of those reproductive parameters that are known to directly influence reproductive success of parasitoids. In the second study, we evaluated the direct effect of floral nectar on the same three parameters, mentioned previously. This experimental set was conducted with flowering species that are native or commonly used in pollinator enhancement and cover crops plantings in Montana. Because sucrose affects longevity and fecundity of these two parasitoid species, the findings of this study could be a step forward in understanding *B. cephi* and *B. lissogaster* reproductive behavior and nutritional requirements. Furthermore, our findings could have important implications in diversifying cropping systems in Montana by identifying, and emphasizing the need to further identify, flowering species to fields that could offer nectar resources to these important parasitoid species.

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CHAPTER TWO

DIFFERENCES IN LONGEVITY, EGG LOAD, AND EGG VOLUME DUE TO
SUCROSE FEEDING IN TWO SYMPATRIC CONGENERIC BRACONIDS THAT
ARE SPECIALIST PARASITOIDS OF THE WHEAT STEM SAWFLY

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Abstract

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is the most important pest of wheat, *Triticum aestivum* L., in the Northern Great Plains of North America. The bivoltine, sympatric and specialist parasitoids *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae), are known to successfully suppress *C. cinctus* populations. However, their occurrence and abundance vary greatly among wheat fields, compromising their effectiveness in reliable management of this serious pest. Studying the life-history strategies that influence reproductive success of these parasitoids could provide useful information to enhance their effectiveness in biological control of *C. cinctus*. Therefore, in this study, we quantified the longevity, egg load, and egg volume of *B. cephi* and *B. lissogaster* to test whether these parameters differ among overwintering and summer generation adult females. We also investigated

the effect of sucrose feeding on the same reproductive parameters. We found no differences between overwintering and summer adults of *B. cephi* and *B. lissogaster*. This indicates that both parasitoid species are well adapted in their bivoltinism. Sucrose had a strong positive effect on longevity and egg load of both species and generations. However, only *B. cephi* females increased egg volume when sucrose was provided. Our results demonstrate the potential of sucrose provision in enhancing the reproductive success of both parasitoid species and generations. This has important implications for successful biological control of *C. cinctus*.

Introduction

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), has long been a pest of major economic importance in wheat in the Northern Great Plains of North America (Beres et al. 2011). Damage caused by this pest recently has expanded southward to parts of Wyoming, Nebraska and Colorado. Damage is caused by the larvae that feed and mine within the plant stem, reducing plant photosynthetic capacity (Macedo et al. 2005; Delaney et al. 2010), kernel weight (Morrill et al. 1994), grain quality, and yield (Morrill et al. 1992, 1994). In addition, at maturity, the larvae cut stems at the base, leaving them susceptible for lodging when exposed to wind or rain (Ainslie 1920, Criddle 1922).

Two sympatric host-specific parasitoids, the larval idiobionts *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae), are known to successfully suppress *C. cinctus* populations in wheat (Morrill et al. 1998, Runyon et al.

2002, Weaver et al. 2004, Beres et al. 2011, Rand et al. 2011, Cárcamo et al. 2012, Buteler et al. 2015). However, their occurrence and abundance vary greatly among wheat fields and regions, compromising their effectiveness in reliable management of this serious pest (Morrill et al. 1998, Cárcamo et al. 2012).

Previous research has revealed several causes for such variation. For instance, high densities of *C. cinctus* populations and heavy tillage are known to decrease parasitoid populations (Holmes et al. 1963). The former is more likely to be associated with the cannibalistic behavior of *C. cinctus* (Holmes et al. 1963, Buteler et al. 2009). Therefore, practices such as minimizing tillage and planting resistant solid-stem wheat cultivars to reduce cannibalism of parasitized conspecifics can enhance parasitoid conservation (Holmes et al. 1963, Runyon et al. 2002, Weaver et al. 2004, Buteler et al. 2015). Despite these efforts, parasitism is still difficult to predict, and detailed information on the life-history of both parasitoid species could contribute to the development of a more effective biological control program against *C. cinctus*.

An interesting aspect of the life-history of *B. cephi* and *B. lissogaster* is that they have two generations per year (bivoltine). The first generation adults, emerge after completing overwinter diapause early in the spring. These individuals have synchronized emergence with *C. cinctus*, but they do not oviposit immediately. There is a pre-oviposition period of 12 to 21 days (Nelson and Farstad 1953, Holmes et al. 1963). After this period is over, females start depositing eggs that will hatch, feed on the host, pupate and emerge as adults in the summer. Females from this second generation start to oviposit almost immediately after emergence (Holmes et al. 1963). Their progeny from

eggs laid later in the season go through overwinter diapause as larvae, and the adults eclose early spring in the following year (Holmes et al. 1963). For both parasitoid species, diapause plays a central role in their life cycles by allowing survival during long and cold winters, as well as synchronizing emergence with host availability. However, diapause could also be costly.

Several authors have suggested a trade-off in the allocation of energy reserves between diapause maintenance and subsequent life-history traits and fitness. For instance, overwintering insects were found to have smaller body size (Sadakiyo and Ishihara 2012), decreased longevity (Larson and Duan 2016) and fecundity (Ishihara and Shimada 1995, Ellers and van Alphen 2002, Sadakiyo and Ishihara 2012, Larson and Duan 2016). However, to overcome energy limitation, adult parasitoids often feed on carbohydrate-derived energy sources, such as the disaccharide sucrose. Feeding on sucrose may benefit parasitoid reproductive success via increasing egg production (England and Evans 1997, Heimpel et al. 1997, Olson and Andow 1998, Tylianakis et al. 2004, Zhang et al. 2011) and longevity which consequently increases searching time and oviposition rate (McDougall and Mills 1997, Schmale et al. 2001, Berndt and Wratten 2005, Lee and Heimpel 2008, Mathews et al. 2007, Nafziger and Fadamiro 2011, Diaz et al. 2012, Géneau et al. 2012, 2013). In the field, parasitoids most commonly obtain sucrose from floral nectar, and there is accumulating evidence for increased parasitoid abundance and parasitism levels in the field in the presence of flowering plants (Stephens et al. 1998, Tylianakis et al. 2004, Lavandero et al. 2005, Berndt et al. 2006, Clough et al. 2011, Simpson et al. 2011, Gurr et al. 2016).

In this study, we quantified the longevity, egg load, and egg volume of the sympatric specialists, *B. cephi* and *B. lissogaster* to test whether these parameters differ among overwintering and summer generation adult females. Moreover, we investigated the effect of sucrose feeding on the expression of those reproductive parameters that are known to directly influence reproductive success of parasitoids. Given the limited knowledge on this subject, our study provides useful information of the life-history trade-offs and nutritional requirements of these closely related parasitoid species that specialize on the same host.

Materials and Methods

Parasitoids

Overwintering generation of *B. cephi* and *B. lissogaster* was collected as prepupae from wheat stubble that was heavily-infested by *C. cinctus* in wheat fields near Amsterdam, Montana, USA (June 2014 and May 2015, 45° 45'32.4"N, 111° 23'49.2"W). Wheat stem samples were dissected and overwintered parasitoid cocoons were collected, stored in plastic bags (16.5 x 14.9 cm) and held at 0-4°C to maintain obligatory diapause. Afterwards, cocoons were placed into glass jars (236 ml), and stored in a growth chamber (E30B, Percival Scientific, Perry, IA) under controlled conditions (25 ± 2 °C, relative humidity 40-60%, and photoperiod 12:12 [L/D] h) until the adults emerged. Jars were checked daily and emerged females were removed and used for greenhouse bioassays. Summer generation parasitoids were reared from ripened winter wheat samples containing parasitoid cocoons. The samples were collected throughout

Montana, USA, in wheat fields near Amsterdam (July 2016, 45° 45'32.4"N, 111° 23'49.2"W), Conrad (July 2015, 48° 1'4.8"N, 110° 15'50.4"W), and Great Falls (July 2016, 47° 30'39.6"N, 111° 6'14.4"W). Ripened samples were placed inside plastic trash barrels (121 liters, 56 x 63 x 71 cm) at room temperature until emergence of parasitoids, which were collected daily and individually placed inside plastic Petri dishes for immediate use in experiments.

Longevity

To test the effect of sucrose feeding on longevity of both generations of *B. cephi* and *B. lissogaster*, newly emerged females were held individually in plastic Petri dishes. Then, individuals were randomly assigned to one of the two treatments: control and sucrose. For control treatment, water was offered through a soaked piece of dental cotton roll (1 x 1 cm, 0.1 g). For sucrose treatment, a 30% (w/v) of sucrose solution was offered as described for water. At this concentration, sucrose has been shown to promote high phagostimulation (feeding response) in parasitoids (Wäckers 1999). Petri dishes were placed inside a growth chamber at 25 ± 2 °C, relative humidity 40-60%, and photoperiod 12:12 (L/D) h. Females were checked daily for mortality and cotton rolls were re-wetted daily. At death, we measured the hind tibia length of the females using a digital micrometer (H-2780, Mitutoyo, Japan), as a measure of parasitoid body size (Jervis et al. 2003). Body size in parasitoids is known to be positively correlated with several key life-history traits, including longevity, egg load and egg volume (Bezemer and Mills 2003, Ellers and Jervis 2003, Saeki and Crowley 2013).

Egg Load and Egg Volume

To determine whether sucrose feeding has an effect on egg load of overwintering and summer generations of *B. cephi* and *B. lissogaster*, we again collected newly emerged parasitoid females and placed them individually in plastic Petri dishes. Prior to experiments, females were randomly assigned to 3 age categories: 2, 6, and 10 days-old. Age categories were then subdivided in two treatment groups: control and sucrose. Water and 30% (w/v) sucrose solution were offered as described above. Petri dishes were kept in controlled conditions (25 ± 2 °C, 40-60% humidity, and 12:12 [L/D] photoperiod) for either 2, 6, or 10 days, as per assigned age categories. Females were freeze killed (-32 ± 1 °C), and body size was determined by measuring the length of the hind tibia using a digital micrometer. Afterwards, parasitoid females were stored in a fixative solution (Kahle's solution - 8 parts 95% ethyl alcohol, 3 parts formalin, 1 part glacial acetic acid to 16 parts of water) (Barbosa et al. 2014). Females were subsequently dissected in ethanol using entomological pins and a stereomicroscope (MZ95, Leica) at 2x magnification. Eggs were removed from the ovaries and mature eggs counted. Only curved sausage shape eggs, tapering toward both poles, were considered mature (Iwata 1959). Under a Dino-Lite digital camera (AM7115MZT-Edge, Dino-Lite, Taiwan) the length and diameter of each mature egg was measured using the software DinoCapture (version 2.0). Volume (V) in μm^3 of each egg was estimated as $V = (\pi r^2) (L - 2r) + (4/3) (\pi r^3)$, where L = length, D = diameter (measured at the midpoint of its long axis) and $r = D/2$ (O'Neill et al. 2014).

Statistical Analysis

All statistical analyses were conducted in R (R Core Team) in conjunction with the integrated development environment R Studio (version 1.0.136) (RStudio Team 2016) (<www.r-project.org>). The effect to sucrose feeding on the longevity of parasitoid females was analyzed using the Kaplan-Meier survival function and log-rank test ('survival' package in R, Therneau and Grambsch 2000). We quantified the effect of age, sucrose, and body size on the egg load of overwintering and summer parasitoid females using generalized linear models (GLM) and logarithmic link function using the 'MASS' package in R (Venables and Ripley 2002). The model included an interaction term for age and sucrose. The negative binomial error distribution was used to account for overdispersion bias associated with egg counts (Sileshi 2006). Additionally, we performed a regression analyses to describe the relationship between egg load and body size of females. We also quantified the effect of age, sucrose and body size on egg volume of both generation adult females of *B. cephi* and *B. lissogaster*. For these data, however, the assumptions of normality and homoscedasticity were met. Thus, we used a linear mixed model (LMM) ('lme4' package) (Bates et al. 2015) treating individual parasitoids as a random factor. Probability values were calculated using log-likelihood ratio tests using the analysis of variance function in the 'car' package (Fox and Weisberg 2011).

Results

Longevity

We found no differences in longevity between overwintering and summer generations of *B. cephi* and *B. lissogaster* (log-rank test: *B. cephi*, $P = 0.1$; *B. lissogaster*, $P = 0.1$). Similarly, there was no significant correlation between longevity and body size of either species and generations (*B. cephi*, $P = 0.57$; *B. lissogaster*, $P = 0.22$). In contrast, sucrose feeding had a strong positive effect on longevity of both species. More specifically, control females of *B. cephi* only lived an average of 10 days, and sucrose fed females lived for an average of 30 days ($P < 0.0001$) (Fig. 1A, B). Control females of *B. lissogaster* lived for a mean of 6 days, whereas females provisioned with sucrose lived for a mean of 52 days ($P < 0.0001$) (Fig. 2A, B).

Egg Load

The egg load of *B. cephi* females was not significantly different between generations ($P = 0.78$). We also found no effect of age ($P = 0.09$) and body size ($P = 0.09$) on the egg load of *B. cephi*. However, sucrose feeding, in this species, significantly increased egg load of both generations ($P < 0.0001$). Maximum egg load was reached after 6 days with an average 4 mature eggs (Fig. 3A). Control females also reached maximum egg load at age 6, but with only one egg (Fig. 2).

In *B. lissogaster*, the egg load of females was significantly affected by generation ($P < 0.05$), positively correlated with body size ($P < 0.0001$) (Fig. 5B), and negatively correlated with age ($P < 0.0001$) (Fig. 2). Overwintering females of *B. lissogaster* had a

significantly larger egg load compared to the summer individuals ($P < 0.05$). However, the egg load of both generations decreased with age. For instance, at day 10 overwintering females had a significant smaller egg load compared to days 2 and 6 ($P < 0.001$) (Fig. 3B). Females of the summer generation had significantly fewer eggs at days 6 and 10, compared to day 2 ($P < 0.001$) (Fig. 3B). Because hosts were absent in this study, our results suggest that *B. lissogaster* females resorb eggs as they age.

Sucrose feeding significantly increased the egg load of both generations of *B. lissogaster* ($P < 0.0001$) (Fig. 3B). Maximum egg load with sucrose feeding was reached after 2 days with 15 mature eggs (Fig. 3B). Control females reached maximum egg load after 2 days, with a mean of 13 mature eggs for overwintering generation, and 12 for summer generation (Fig. 3B).

Egg Volume

The variables age (LMM, $P = 0.36$) and body size ($P = 0.09$) did not affect egg volume of overwintering and summer adult females of *B. cephi*. In contrast, sucrose feeding significantly affected egg volume in this species ($P < 0.0001$), with an estimated increase of $0.0089 \mu\text{m}^3 \pm 0.0015$ (SE) compared to the control (Fig. 4A). For *B. lissogaster* any of the variables affected egg volume of overwintering and summer adult females (age, $P = 0.09$; body size, $P = 0.28$; sucrose, $P = 0.1$) (Fig. 4B).

Discussion

Overall, our results showed no differences in longevity, egg load, and egg volume between overwintering and summer generations of *B. cephi* and *B. lissogaster*. These suggest that both parasitoid species are well adapted to long, cold winters and short, hot dry summers in their bivoltinism. In contrast, sucrose feeding had a strong positive effect on the reproductive biology of both parasitoid species and generations. Our findings also highlighted the contrasting life histories of these two sympatric, specialist parasitoids. These differences may have important implications on successful biological control of *C. cinctus*.

Several authors have suggested a trade-off in the allocation of energy reserves between diapause maintenance and subsequent life-history traits and fitness (Denlinger 1979, Danks 1987, Ishihara and Shimada 1995, Ellers and van Alphen 2002, Larson and Duan 2016). Although in *B. lissogaster*, the egg load of overwintering adults was significantly higher than in summer individuals, these results may be due to the strong effect of age (Fig. 4B). Younger females carry more eggs than older ones, demonstrating that egg resorption occurs in *B. lissogaster* females as they age. Overwintering females start egg resorption later in their lifespan, thus they resorb fewer eggs than summer females. Egg resorption is a common reproductive strategy among parasitoids (Bell and Bohm 1975), and it can be a means of eliminating defective oocytes, maintaining a constant supply of newly mature eggs, and/or recycling resources during periods of nutrient stress (King and Richards 1968, Bell and Bohm 1975, Collier 1995, Rivero-

Lynch and Godfray 1997). More recently, egg resorption has been proposed to be an insurance against stochasticity (Richard and Casas 2009). Parasitoid females cannot control the rate of host encounter, and in highly stochastic environments, the risk of dying before finding a host increases (Rosenheim et al. 2000). However, females can control when to resorb eggs, and, therefore, they control the timing of their future energy gain, despite availability of alternative food resources (Richard and Casas 2009). Thus, through egg resorption, female parasitoids can survive to forage longer and thus increase their chances to oviposit even at low host densities (Richard and Casas 2009).

The relationship between body size and reproductive success in parasitoids has been studied extensively. Under laboratory conditions, parasitoid body size positively correlates with longevity, egg load and oviposition rate (Visser 1994, Saeki and Crowley 2013). In the present study, body size was only positively correlated with egg load in *B. lissogaster* females (Fig. 5B). These results may suggest that larger females have an increased reproductive capacity than smaller conspecifics. However, the positive effect of body size on increased egg load of *B. lissogaster* females may be of limited importance if there are many factors contributing to parasitoid mortality in the field. Thus, the use of cultural practices that support conservation of parasitoids is essential to increase their effectiveness. Previous studies suggest that producers should minimize tillage and cut wheat high, leaving at least two thirds of the stem in the field to reduce mortality of *Bracon* spp. which are overwintering above ground in standing stems, and would otherwise be killed during such operations (Runyon et al. 2002, Meers 2005, Beres et al. 2011).

Moreover, the positive correlation between body size and egg load in *B. lissogaster* could also be associated with immature development. The larvae of this species can develop either solitary or gregariously (Somsen and Luginbill 1956), and when more than two parasitoids are feeding on the same host, immature development time is reduced and individuals are smaller than those that feed solitarily (Somsen and Luginbill 1956). In contrast, *B. cephi* is solitary, and only one egg is laid per host (Nelson and Farstad 1953). Interestingly, we found that only *B. cephi* can increase egg volume with sucrose feeding. The implications of such results still need to be investigated, however, in a study comparing immature developmental rates of two congeneric parasitoids, Donnel and Hunter (2002) showed that larger eggs hatch earlier than smaller ones. Being the first larvae to hatch could be advantageous in terms of early utilization of the host resources (Parker and Begon 1986, Harvey et al. 2013). Thus, by increasing egg volume with sucrose, females of *B. cephi* could be providing an advantage in competition for their progeny. In *B. lissogaster*, the amount of resources invested in egg volume seems to be fixed, regardless of body size and sucrose supplementation (Fig. 4B).

We found an interesting contrast in egg load between the two braconid species. Control females of *B. cephi* carried an egg load that was 13 times smaller than for *B. lissogaster* individuals (Fig. 4A, B). Although this difference decreased with sucrose feeding, *B. cephi* females still carried four times fewer eggs than *B. lissogaster* (Fig. 4A, B). These differences in life-history could be associated with the mechanisms that allow coexistence of these species in the habitat. Theory predicts that superior competitors typically have limited fecundity, and hence, they are unable to explore all the resources

available, leaving gaps that inferior competitors can exploit (Bolker and Pacala 1999). In contrast, competitively inferior species have increased fecundity and are able to disperse offspring before superior competitors arrive (the fugitive strategy, Bolker and Pacala 1999). As a result, intra-specific clusters are formed, increasing the strength of intra-specific competition relative to inter-specific competition, and allowing coexistence (Amarasekare 2003). Thus, life-history differences allow coexistence by creating spatial niche differences between species that in turn arise from intra-specific clustering and inter-specific segregation (Amarasekare 2003). This may explain why *B. lissogaster* females carry a high egg load, and yet *B. cephi* is the most abundant species parasitizing *C. cinctus* larvae in the field (Beres et al. 2011).

Finally, Rand et al. (2017) suggests that 68% parasitism is necessary to sufficiently suppress *C. cinctus* populations. In some fields parasitism rates can reach up to 79% (Weaver et al. 2004). However, increased percentages of parasitism can best be achieved in an integrated manner, for instance by planting solid stem wheat in fields where *C. cinctus* infestation is high (Beres et al. 2011), and tillage is reduced (Runyon et al. 2002). In the present study, we found no differences between overwintering and summer generations of *B. cephi* and *B. lissogaster*, and both species and generations greatly benefit from sucrose feeding. Therefore, our results suggest that sucrose supplementation may also contribute to maintain high levels of *C. cinctus* parasitism. However, these effects remains to be investigated in the field.

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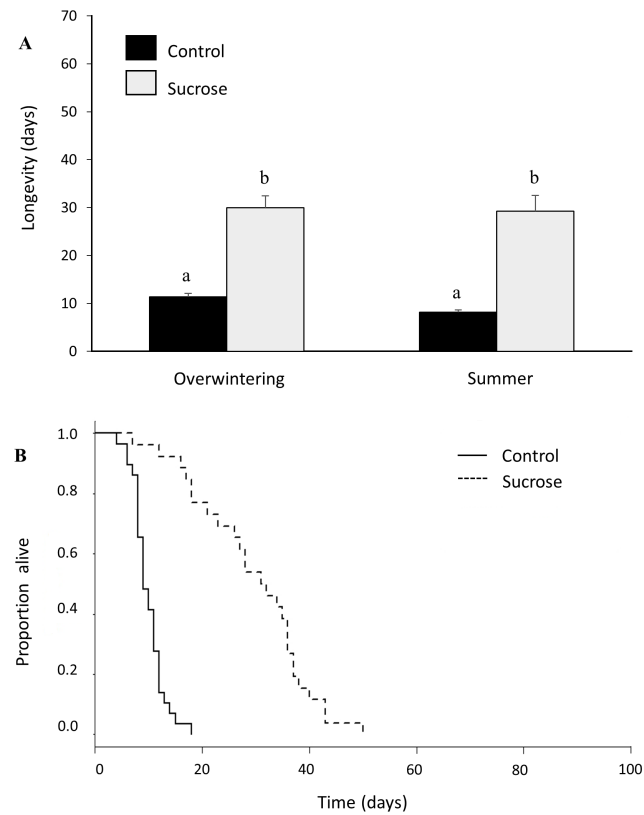


Fig. 2.1. Longevity of *B. cephi* females provided water (control) or sucrose solution. Treatments were offered *ad libitum* to parasitoids that were assessed daily for mortality. Survival in days is represented in (A) mean $\pm$ SE, and (B) Kaplan-Meier probability curves. Bars followed with the same letter indicate no significant differences ($P > 0.05$); $n = 55$.

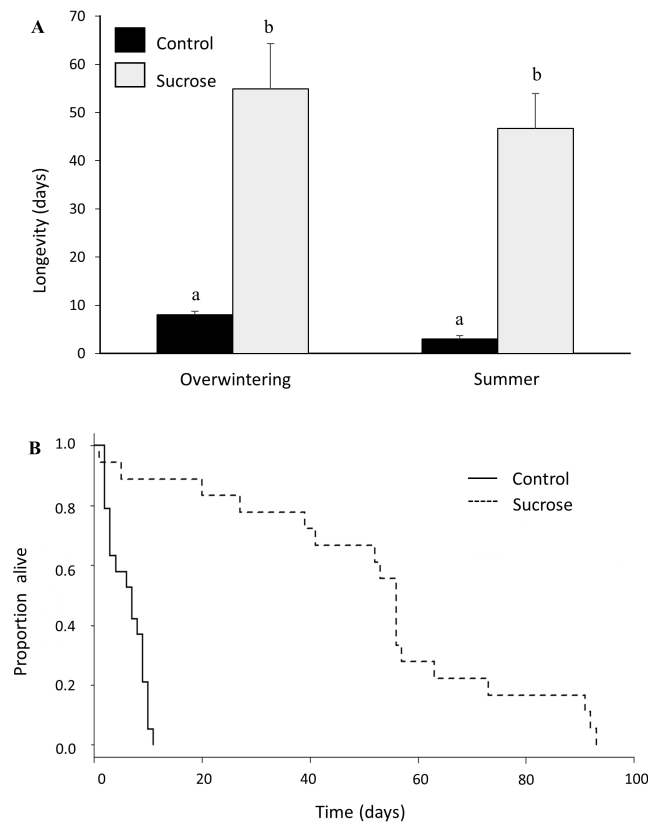


Fig. 2.2. Longevity of *B. lissogaster* females provided water or sucrose. (A) Mean $\pm$ SE survival of parasitoids in days, and (B) Kaplan-Meier survival probability curves. Bars followed with the same letter indicate no significant differences ($P > 0.05$); ($n = 37$).

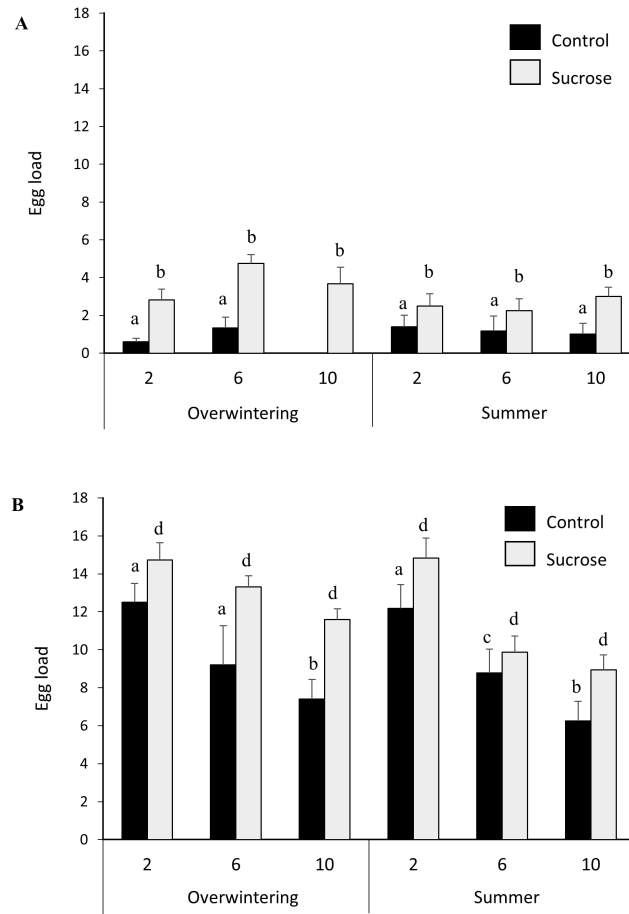


Fig. 2.3. Mean ($\pm$ SE) egg load of overwintering and summer adult parasitoid females provided water or sucrose solution. Diets were offered *ad libitum* for 2, 6 and 10 days. (A) *B. cephi* (overwintering $n = 60$; summer $n = 23$) and (B) *B. lissogaster* (overwintering $n = 61$; summer $n = 76$). Bars followed with the same letter indicate no significant differences ($P > 0.05$) based on statistical analysis using likelihood-ratio tests (LRT) and generalized linear models (GLM).

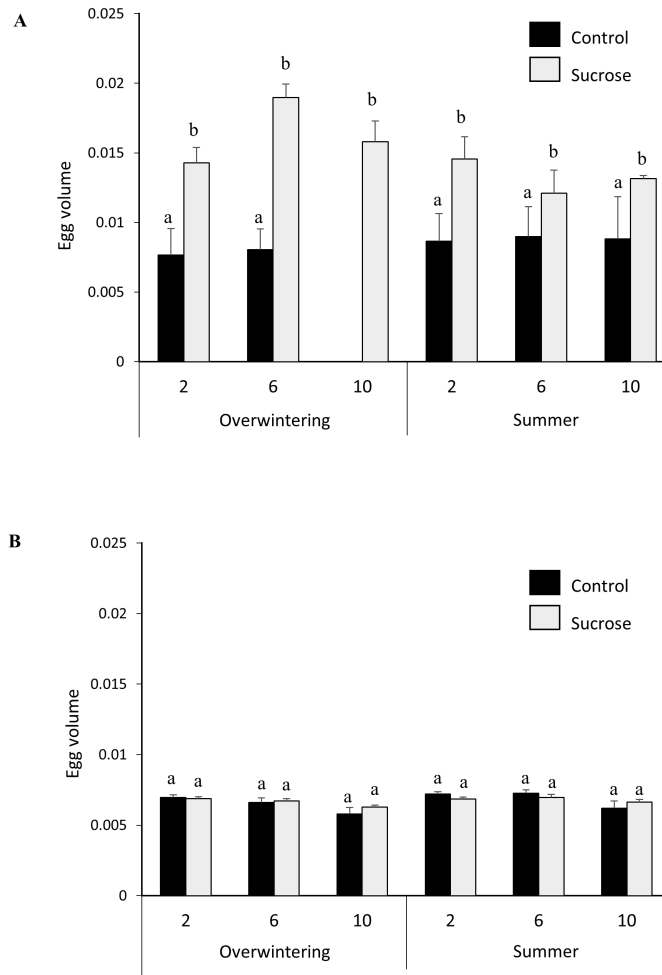


Fig. 2.4. Mean ($\pm$ SE) of egg volume (μm^3) of (A) *B. cephi* and (B) *B. lissogaster*. Overwintering and summer adult females of both parasitoid species were provided water or sucrose for 2, 6 and 10 days. Bars followed with the same letter indicate no significant differences ($P > 0.05$) based on statistical analysis using linear mixed models (LMM); *B. cephi* (overwintering $n = 60$, summer $n = 23$); *B. lissogaster* (overwintering $n = 61$; summer $n = 76$).

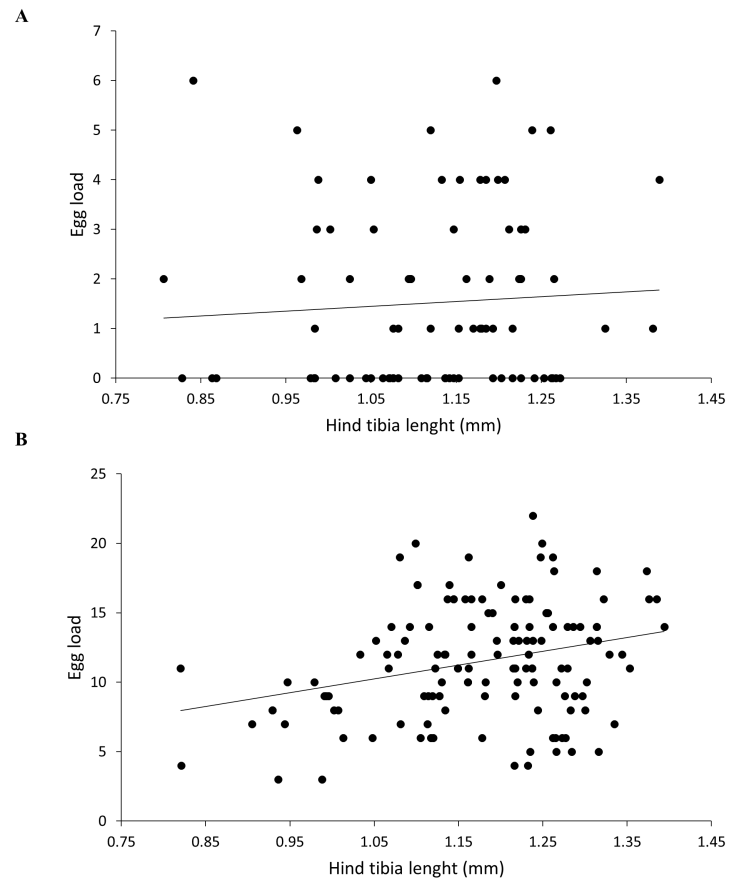


Fig. 2.5. Scatterplot of the relationship between egg load and body size in both generations of (A) *B. cephi* ($n = 83$) ($P = 0.09$) and (B) *B. lissogaster* females ($n = 137$) ($P < 0.0001$).

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CHAPTER THREE

THE EFFECT OF CULTIVATED AND NATIVE FLORAL SPECIES AS
RESOURCES IN THE REPRODUCTIVE BIOLOGY OF WHEAT STEM SAWFLY
PARASITOIDS

Contribution of Authors and Co-Authors

Manuscript in Chapter Three

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Contributions: Conceived and designed experiments, collected and processed experimental data, analyzed and interpreted results, and wrote manuscript for journal submission.

Co-Author: Robert K. D. Peterson

Contributions: Collaborated in interpretation of results and manuscript preparation.

Co-Author: Megan L. Hofland

Contributions: Collaborated in data acquisition and provided insects for experiments.

Co-Author: David K. Weaver

Contributions: Conceived and designed experiments, provided critical input at all stages of experiment including interpretation of results and manuscript preparation.

Manuscript Information Page

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CHAPTER THREE

THE EFFECT OF CULTIVATED AND NATIVE FLORAL RESOURCES ON THE
REPRODUCTIVE BIOLOGY OF WHEAT STEM SAWFLY PARASITOIDS

The following chapter has been prepared for submission to a peer-reviewed journal

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Abstract

One of the goals of conservation biological control is to enhance natural enemy populations in crop habitats by providing flowering plants as food resources. However, a flowering species must be both beneficial to the insect natural enemy, and practical for producers for it to be considered suitable. Therefore, in this study we evaluated buckwheat (*Fagopyrum esculentum*), lacy phacelia (*Phacelia tanacetifolia*), deerhorn clarkia (*Clarkia pulchella*), canola (*Brassica napus*) and safflower (*Carthamus tinctorius*) for their potential to increase longevity, egg load and egg volume of *Bracon cephi* and *B. lissogaster*, the two most important parasitoids of wheat stem sawfly, *Cephus cinctus*. These flower species were selected based on use in pollinator enhancement via native species restoration or their role in alternative or cover crops in Montana. We found that longevity of *B. cephi* females was significantly increased with access to flowering buckwheat and safflower, and egg load and egg volume increased with buckwheat and

deerhorn clarkia. Females of *B. lissogaster* had increased egg loads with access to flowers of deerhorn clarkia. The results suggest that species with sucrose rich nectar, such as buckwheat, may provide the greatest benefit to reproduction of *B. cephi*. However, alternative or cover crop safflower, and native deerhorn clarkia may be preferable for producers, as the former species provides an economic value, and the native is historically distributed. This may reduce the risk of undesirable contamination in Montana wheat crops associated with buckwheat. This study demonstrates that suitable floral species are of benefit in the reproductive biology of parasitoids vital to the biological control of *C. cinctus*.

Introduction

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) is a native species of North America that was first identified in the western part of the country as a pest of large-stemmed native grasses (Ainslie 1920). However, as European settlers began to farm shortgrass prairie, large areas of native grasses were displaced to cultivate wheat, *Triticum aestivum* L., and *C. cinctus* rapidly adapted to this new and widely distributed plant host (Fletcher 1896). Currently, the wheat stem sawfly is the most destructive pest of wheat in the Northern Great Plains of North America (Beres et al. 2011), and most recently, damage resulting from this pest has expanded southward into parts of Colorado, Nebraska and Wyoming. Damage to wheat is caused by the stem-mining larvae that feed and develop inside the stems, reducing plant photosynthetic capacity (Macedo et al. 2005), kernel weight (Morrill et al. 1994), grain quality, and yield

(Morrill et al. 1992, 1994). In addition, at maturity, the larvae cut the stems at the base, leaving them susceptible for lodging when exposed to wind or rain (Criddle 1922, Munro 1945).

A total of 10 species have been reported to parasitize *C. cinctus* in native or feral grasses (Criddle 1923, Marsh 1979, Morrill et al. 1998), but only two specialist species, the native larval idiobionts *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae), are known to commonly parasitize *C. cinctus* larvae in wheat (Davis et al. 1955, Somsen and Luginbill 1956, Morrill et al. 1994). In Montana, both parasitoid species are known to successfully suppress *C. cinctus* populations (Morrill et al. 1998, Runyon et al. 2002, Weaver et al. 2004, Beres et al. 2011, Rand et al. 2011, Buteler et al. 2015) and reduce economic losses (Buteler et al. 2008). However, their occurrence and abundance is highly variable across wheat fields and regions, making them inconsistent in overall management of this important insect pest (Morrill et al. 1998).

The conversion of natural habitats for agricultural use is known to negatively affect natural enemy populations (Landis and Menalled 1998, Landis et al. 2000, Benton et al. 2003, Gurr et al. 2004, Rusch et al. 2016). This is because oversimplified agricultural landscapes often do not provide important resources for natural enemies such as food, alternative hosts and refuges (Landis et al. 2000, Bianchi et al. 2006, Fiedler et al. 2008, Chaplin-Kramer et al. 2011). Conservation biological control is a habitat management strategy used to enhance the abundance and effectiveness of natural enemies in agricultural landscapes (Barbosa 1998, Landis et al. 2000, Gurr et al. 2017). This

includes the provision of nectar producing flowering plants as suitable sources of carbohydrate rich foods (Gurr et al. 2004). Laboratory experiments with *B. cephi* and *B. lissogaster* have shown that females increase longevity and egg load when sucrose is provided (Reis et al. in preparation). Egg volume has also increased in *B. cephi* when fed sucrose (Reis et al. in preparation). Therefore, if floral nectar has a similar effect on reproduction of *B. cephi* and *B. lissogaster*, this may lead to greater parasitism and improved biological control of *C. cinctus*.

In the present study, greenhouse experiments were conducted to investigate the suitability of five flowering plant species to increase the longevity, egg load and egg volume of females of *B. cephi* and *B. lissogaster*. We selected buckwheat (*Fagopyrum esculentum* Moench, Polygonaceae) and lacy phacelia (*Phacelia tanacetifolia* Benth, Hydrophyllaceae) based on their positive effect on many natural enemies and frequent use in habitat management studies (Lee et al. 2004, Lavandero et al. 2006, Fiedler et al. 2008, Balzan and Wäckers 2013, Araj and Wratten 2015). However, these plants are not native, which is important criterion in the restoration of critical habitat for pollinators. Therefore, we also included the western native deerhorn clarkia (*Clarkia pulchella* Pursh, Onagraceae) (Craighead et al. 1963). The alternative or cover crops canola (*Brassica napus* L., Brassicaceae) and safflower (*Carthamus tinctorius* L., Asteraceae) were also evaluated. Little is known about the potential of the native and crop species as nectar sources for parasitoids in this agroecosystem. Also, there is increasing interest in growing these species as cover crops in Montana (Jones et al. 2016). Although these crops are typically grown primarily for profit, not as cover crops for soil protection and soil

enrichment (Lu et al. 2000), at bloom these plants could also be a source of nectar to parasitoids.

Materials and Methods

Insects

Bracon cephi and *B. lissogaster* larvae were collected in wheat fields that were heavily infested by *C. cinctus* near Amsterdam (45° 45'32.4"N, 111° 23'49.2"W), Big Sandy (48° 10'51.6"N, 110° 20'34.8"W) and Great Falls (47° 30'39.6"N, 111° 6'14.4"W) in Montana, USA. Ripe wheat samples, containing the summer generation of non-diapause parasitoid larvae, were placed inside plastic trash cans (121 liters, 56 x 63 x 71 cm) and kept at room temperature until emergence of parasitoids. Samples with postharvest larvae in the overwinter generation were placed in plastic bags and held at 0-4° C for 100 days to facilitate completion of the obligatory diapause. After at least 100 days had passed, samples were placed inside plastic boxes (27.5 liters, 41 x 33 x 22 cm) and kept at room temperature. All samples were inspected daily and newly emerged adults were removed and individually placed inside plastic Petri dishes.

Plant Culture

Bioassays assessing the effect of flower resources on the longevity and fecundity of *C. cinctus* parasitoids were performed inside an even span greenhouse (12.19 x 21.95 m) at Montana State University Plant Growth Center (MSU-PGC, Bozeman, MT, USA). The plant species were buckwheat, lacy phacelia, deerhorn clarkia, canola and safflower.

Each plant species was sown weekly in square pots (13 x 13 x 13.5 cm), kept under natural and artificial light (GE Multi-vapor lamps model MVR1000/C/U, GE Lighting, General Electric Co., Cleveland, OH), with a 14:10 (L:D) h photoperiod, 22 ± 2 °C and maintained at 20-40% RH. Plants were watered daily and fertilized weekly with Peters General Purpose Fertilizer (J.R. Peters, Allentown, PA) at 100 ppm in aqueous solution. Soil consisted of equal parts MSU-PGC soil mix and Sunshine Mix1. The MSU-PGC soil mix consisted of equal parts sterilized Bozeman silt loam soil, washed concrete sand and Canadian sphagnum peat moss. Sunshine Mix 1 consisted of Canadian sphagnum peat moss, perlite, vermiculite, and Dolomitic lime. Plants were used for experimentation at the initiation of bloom.

Experimental Design

To test whether floral resources enhance the longevity, egg load, and egg volume of *B. cephi* and *B. lissogaster*, newly emerged parasitoid females were randomly assigned and individually placed inside cages with newly bloomed flowers. Control females were released inside empty cages with only water availability. The cages were made of plastic cocktail cups (226 ml). The bottom part of the cup was removed and covered with a tulle fabric (0.3-mm mesh) to allow ventilation while preventing escape of parasitoids. On the other side of the cup, another piece of tulle fabric was glued and used to close the cage. The cups were tied to a wooden rod with a twist-tie, and inserted into the soil near the plants. Water was provided through a soaked piece of cotton roll placed on the top of

each cage. Due to limited numbers of adult females emerging daily, treatments were randomized across dates.

For each of the treatments, 12 parasitoids of each species were tested. According to the results found by Reis et al. (in preparation), females from overwintering and summer generations were pooled for use in the experiment. Cages were inspected daily to assess mortality and cotton rolls were re-wetted at this time. At death, females were preserved in a 0.5 ml Eppendorf tube containing Kahle's fixative solution: which was (v/v): 8 parts 95% ethyl alcohol, 3 parts formalin, 1 part glacial acetic acid to 16 parts of water (Barbosa et al. 2014). Specimens were subsequently dissected in ethanol with entomological pins while under stereomicroscopic magnification.

Eggs were removed from the ovaries, and only curved sausage-shaped oocytes, tapering toward both poles, were considered mature (Iwata 1959). Under a Dino-Lite digital camera (AM7115MZT-Edge, Dino-Lite, Taiwan) the length and diameter of each mature egg was measured using the software DinoCapture (version 2.0). The volume (V) in μm^3 of each egg was estimated as $V = (\pi r^2) (L-2r) + (4/3) (\pi r^3)$, where L = length, D = diameter (measured at the midpoint of its long axis) and $r=D/2$ (O'Neill et al. 2014).

Statistical Analyses

All statistical analyses were performed in R (R Core Team) along with the integrated development environment RStudio (version 1.0.136) (RStudio Team 2016) (<www.r-project.org>). We used the 'car' package to test for outliers (Fox and Weisberg 2011) and Leverage values and Cook's distance to check for influential observations (Chatterjee and

Hadi 1986). Visual inspection of the residuals was used to determine if data were normally distributed and homoscedastic. Some data did not satisfy the assumptions of homogeneity of variance (Levene's test, $P < 0.05$) and therefore were log-transformed. However, untransformed data are presented. To test whether flower species had a positive influence on longevity of *B. cephi* and *B. lissogaster* we performed one-way analysis of variance with flower species as a factor followed by an F test. Data on egg load and egg volume of both parasitoid species failed the assumptions of normality and homogeneity of variances, even after log-transformation. Hence, these data were analyzed using Kruskal-Wallis and Dunn's post-hoc test ('dunn.test' package, Dinno and Dinno 2017). All tests were performed at $\alpha = 0.1$.

Results

Of the five floral species tested, only buckwheat ($P < 0.01$) and safflower ($P < 0.1$) inflorescences significantly increased the longevity of *B. cephi* compared to control. The mean longevity of female parasitoids was 26 days with buckwheat, and 13 days with safflower compared to control females at 7 days. The longevity of *B. lissogaster* females did not increase with any of the floral species tested (Fig.1).

We found that access to buckwheat (Dunn's test, $z = -3.847$, $P < 0.001$) and deerhorn clarkia (Dunn's test, $z = -2.293$, $P < 0.05$) significantly increased the egg load of *B. cephi*. Control females had a mean of 0.17 eggs, and females with access to buckwheat and deerhorn clarkia inflorescences had 1.58 and 0.91 eggs, respectively (Fig. 2). The egg volume of *B. cephi* females was also significantly greater with access to

buckwheat (Dunn's test, $z = -3.988$, $P < 0.001$) and deerhorn clarkia inflorescences (Dunn's test, $z = -2.04$, $P < 0.05$) (Fig 3). In *B. lissogaster*, the egg load significantly increased with deerhorn clarkia (Dunn's test, $z = -1.595$, $P < 0.1$). Control females had a mean of 7 eggs compared to 9 eggs with access to flowering deerhorn clarkia. However, access to floral resources did not increase the egg volume of *B. lissogaster* females (Kruskal-Wallis test, $\chi^2 = 1.24$, $P > 0.1$).

Discussion

In this study, we provided buckwheat, lacy phacelia, deerhorn clarkia, canola, and safflower inflorescences to assess possible increases in longevity, egg load, and egg volume of *B. cephi* and *B. lissogaster*, the two most important parasitoid species of *C. cinctus*. We found that only buckwheat and safflower had a positive effect on the longevity of *B. cephi* females. Access to buckwheat and deerhorn clarkia inflorescences increased both egg load and egg volume of *B. cephi*, and deerhorn clarkia increased egg load of *B. lissogaster*. The mechanisms underlying these findings require further investigation. It is unknown if the observed effects in longevity, egg load, and egg volume are a result of differences in nectar nutritional quality or constraints on accessibility.

Floral nectar mainly comprises the sugars sucrose, glucose, and fructose (Baker and Baker 1983). These sugars have been shown to have the greatest positive effect on the longevity of parasitoids (Wäckers 2001) due to their easy convertibility to energy sources (Hausmann et al. 2005). However, the ratio of these sugars in the nectar

composition could also play an important role on the survival responses of parasitoids. For instance, some species were found to live longer with sucrose dominant nectars than with glucose or fructose rich nectars (Vattala et al. 2006, Varennes et al. 2016, Nave et al. 2017). Moreover, some studies have suggested that nectars with high fructose and glucose ratio may disrupt the water balance of parasitoids, and therefore are less preferred due to physiological constraints (Baker and Baker 1983, Blüthgen and Fiedler 2004, Vattala et al. 2006). Other studies, however, showed no differences in longevity of parasitoids regarding the ratio of those sugars in the nectar composition (Tompkins et al. 2010, Furtado et al. 2016). Our results showed that the longevity of *B. cephi* significantly increased with access to buckwheat and safflower inflorescences, however, females lived twice as long on buckwheat (Fig. 1). The nectar of this floral species is known to be sucrose dominant (Vattala et al. 2006, Tompkins et al. 2010), and our results agree with many studies showing that buckwheat is a superior food source compared to other floral species (Fiedler et al. 2008, Russell 2015). In contrast, little is known about safflower nectar quality. Nonetheless, our results suggest that this floral species that is used in cover crop plantings and as an alternative crop, is also a good candidate for possibly enhancing conservation biological control of *C. cinctus* parasitoids.

The egg load of *B. cephi* females increased with access to both buckwheat and deerhorn clarkia flowers (Fig. 2). Feeding on floral resources may directly increase fecundity of parasitoids by increasing egg production (Heimpel et al. 1997, Tylianakis et al. 2004, Zhang et al. 2011). Fecundity may also increase indirectly as a consequence of increased longevity, and therefore, extra time for egg maturation (Giron et al. 2002,

Berndt and Wratten 2005, Lee and Heimpel 2008, Géneau et al. 2012). Buckwheat nectar greatly increases longevity of *B. cephi* females (Fig. 1), and because this parasitoid species is synovigenic (egg maturation continues during the adult life) (Jervis et al. 2001, Reis et al. in preparation), more eggs can mature in females that live longer. The increase in egg load with buckwheat nectar could be due to a positive effect of this flower on longevity rather than a direct increase in fecundity due to improved nutrition. In general, insects that feed on sugar rich nectars immediately use those resources to increase longevity (reviewed in Rivero and Casas 1999, Heimpel and Jervis 2005, Wäckers 2005, Benelli et al. 2017). Conversely, insect species that feed on amino acid-rich nectars directly invest these nutrients in egg production (Nicolson and Thornburg 2007, Panizzi and Parra 2012). Our results showed that deerhorn clarkia nectar significantly increased egg load of *B. cephi* and *B. lissogaster* (Fig. 2). However, we found no effect of this floral nectar on the longevity of parasitoids, suggesting that nectar of this native floral species might be rich in amino acids.

Our results also showed that *B. cephi* significantly increased egg volume with access to buckwheat and deerhorn clarkia flowers (Fig. 3). Increased egg size could provide a competitive advantage during larval development. Larger eggs hatch earlier (Donnell and Hunter 2002), and older larvae can monopolize host resources (Harvey et al. 2013). This might be of considerable importance for *B. cephi* since the immatures develop solitarily on the host (Nelson and Farstad 1953). Previous research has shown that sucrose feeding enhances egg volume of *B. cephi* females, and this may provide a competitive advantage for their progeny (Reis et al. in preparation). However, the results

of this study show that sucrose, and potentially nectar amino acids could play a similar role in fitness of female parasitoids.

Access to lacy phacelia did not enhance longevity and fecundity of *B. cephi* and *B. lissogaster*. These results are probably due to flower morphology. Phacelia nectaries are located at the bottom of a deep (10 – 15 mm) corolla which entrance is covered by scales (Verennes et al. 2016). This flower morphology may have nectar that is limited in accessibility for exploitation by these parasitoids. Other species have also been shown to be unable to consume lacy phacelia nectar from the flowers (Vattala et al. 2006, Verennes et al. 2016), illustrating the importance of floral morphology for nectar exploitation by parasitoids (Patt et al. 1997).

We also found no effect of canola on reproduction of both parasitoid species. Although canola flowers are capable of self-pollination, the inflorescences produce abundant nectar that attracts and rewards floral visitors (Free and Nuttall 1968). This crop species benefits from insect visitation with increased yield (Morandin and Winston 2006, Bommarco et al. 2012, Bartomeus et al. 2014). Many insects are known to benefit from canola nectar (Russell 2015), however, this floral species did not enhance any of the reproductive parameters tested in *B. cephi* and *B. lissogaster*. A possible explanation for these results is that canola nectar is glucose dominant (Carruthers et al. 2017). As mentioned above, glucose rich nectars may cause physiological constraints in parasitoids (Baker and Baker 1983, Vattala et al. 2006), and this is an important factor influencing parasitoid dietary selection (Blüthgen and Fiedler 2004). Thus, nectar quality could have

played an important role on the suitability of canola inflorescences to *B. cephi* and *B. lissogaster*. This potential limitation merits further investigation.

The success of habitat management for enhancing the impact of parasitoids on agricultural insect pests depends on selection of adequate flower species that should not only provide resources to enhance longevity and fecundity of parasitoids, but also be practical for producers to grow (Landis et al. 2000, Gurr et al. 2017). Although buckwheat seems to be a suitable candidate species to enhance conservation biological control of *B. cephi*, it currently may not be the best option for producers. In a number of western states, including Montana, the Natural Resources and Conservation Service (NRCS) has temporarily excluded buckwheat from conservation plantings adjacent to commodity wheat production, due to its potential to contaminate the wheat crop and the human allergen health risks that buckwheat seed poses (USDA-NCRS 2016). In contrast, safflower and deerhorn clarkia may be of greater benefit for producers, as the cover crop species can provide an economic return, and the native species is commonly found in the Pacific Northwest (Craighead et al. 1963), and is also commonly included in native seed mixtures for prairie restoration projects (Matt 2015).

In conclusion, we have provided evidence that females of *B. cephi* that can access buckwheat and safflower inflorescences have increased longevity, and buckwheat and deerhorn clarkia nectar likely increases egg load and egg volume. For *B. lissogaster*, access to deerhorn clarkia flowers enhanced egg load. These results suggest that flowers containing sucrose-rich nectar, such as buckwheat, may provide the highest benefit to reproduction of *B. cephi*. However, the utilization of the native species, deerhorn clarkia,

may benefit both *B. cephi* and *B. lissogaster*, and it could be more practical for producers because it is commonly use in restoration and is broadly distributed. There is no risk of crop contamination, a key concern for buckwheat. Further research is needed to clarify the role of nectar quality and flower morphology on these parasitoids before broadly including these plants in habitat management strategies. Those future findings will be of importance in making decisions for conservation biological control of *B. cephi* and *B. lissogaster* and to improve the impact of these parasitoids on *C. cinctus* populations.

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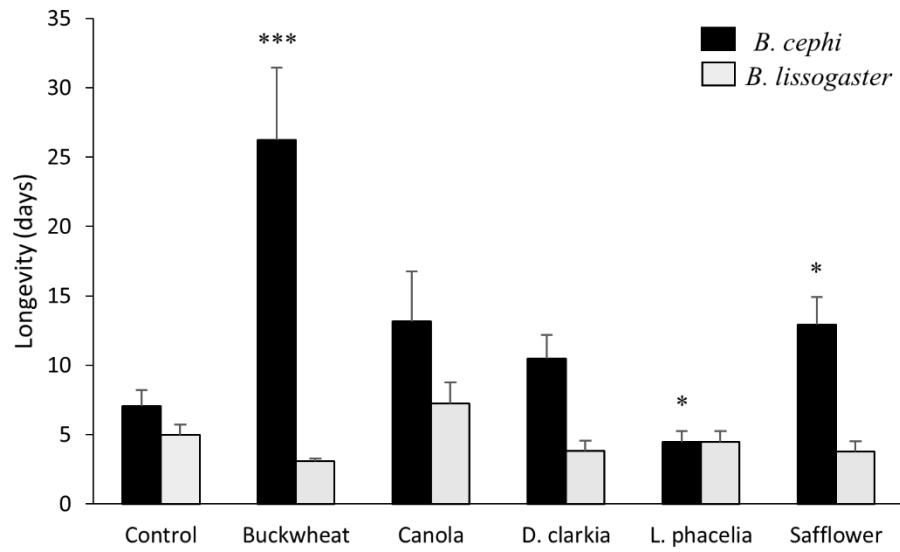


Fig. 3.1. Mean $\pm$ SE longevity of *B. cephi* and *B. lissogaster* females tested with flower species that are used in crops and for increased pollinator resources *** and * indicate significant differences compared to control treatment ($P < 0.01$ and $P < 0.1$, respectively) based on one-tailed F-test at $\alpha = 0.1$ ($n = 12$).

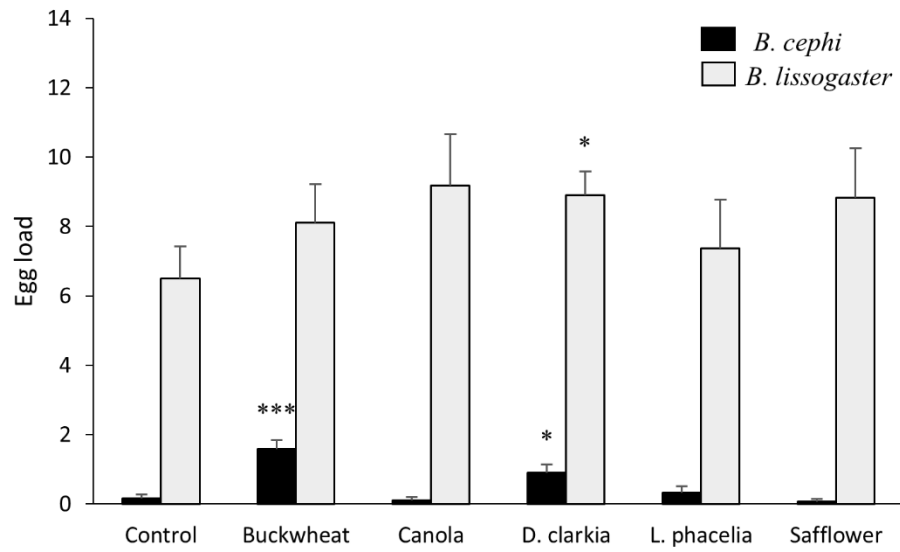


Fig. 3.2. Mean $\pm$ SE egg load of *B. cephi* and *B. lissogaster* females tested with buckwheat, lacy phacelia, deerhorn clarkia, canola and safflower. *** and * indicate significant differences compared to control treatment ($P < 0.01$ and $P < 0.1$, respectively), based on Kruskal-Wallis test followed by Dunn's test at $\alpha = 0.1$ ($n = 12$).

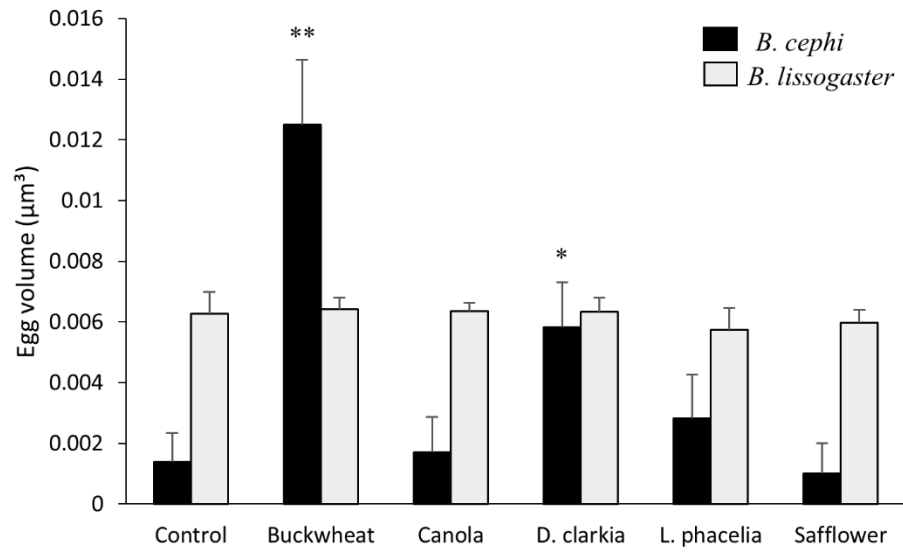


Fig. 3.3. The effect of access to nectar of five flowering species on the egg volume (mean $\pm$ SE) (μm^3) of *B. cephi* and *B. lissogaster*. ** and * indicates significant differences ($P < 0.01$ and $P < 0.05$) based on Kruskal-Wallis test followed by Dunn's test at $\alpha = 0.1$ ($n = 12$).

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CHAPTER FOUR

CONCLUSION

This research investigated the effects of artificial and natural sugar resources on the reproductive physiology of *Bracon cephi* and *B. lissogaster*, the two most important parasitoids of *Cephus cinctus*. This information could be of considerable benefit in diversification of cropping systems in Montana and elsewhere, which now includes nectar-producing crops. Additionally, we investigated how reproductive traits differ among overwintering and summer generations of *B. cephi* and *B. lissogaster*. This basic knowledge will aid in the understanding of life-history strategies used by these beneficial insects to persist under adverse conditions.

In chapter 2, we provided a sucrose solution to overwintering and summer generation adult females of both species, and quantified and compared the longevity, egg load, and egg volume. This study revealed that reproduction of *B. cephi* and *B. lissogaster* did not differ between overwintering and summer generations.

We found a strong positive effect of sucrose feeding on survival and fecundity of these species. Interestingly, this effect was different between species. For *B. cephi*, sucrose feeding increased longevity, egg load and egg volume. Whereas, for *B. lissogaster* sucrose only increased longevity and egg load. The investment of resources to increase egg volume in *B. cephi* may reflect an adaptation to optimize fitness. In this species, immatures develop solitarily and larger eggs have a greater probability of survival. For *B. lissogaster*, with immature stages that can develop gregariously, egg

volume did not change. Another interesting finding provided by this study is that *B. lissogaster* females are probably capable of egg resorption, and that both parasitoid species are synovigenic.

Because *B. cephi* is known to be the most abundant species parasitizing *C. cinctus* larvae in the field, we expected that females of this species would carry more eggs than *B. lissogaster*, especially after overwinter diapause. However, our results showed that *B. cephi* carries a smaller load of mature eggs than *B. lissogaster*. These differences might underlie the mechanisms that allow coexistence of these sympatric congeners in wheat fields. Spatial competition theory predicts that superior competitors typically have limited fecundity, and hence, they are unable to exploit all the resources available, leaving gaps that inferior competitors can exploit. In contrast, competitively inferior species have increased fecundity and are able to disperse offspring before superior competitors. Consequently, intraspecific clusters are formed, increasing the strength of intraspecific competition relative to interspecific competition, and allows coexistence. Thus, life-history differences may allow coexistence of these species, *B. cephi* and *B. lissogaster*, that share a single common host. Overall, this study highlights differences in reproductive strategies between specialist congeneric parasitoids that are almost identical in appearance and fully sympatric, while also demonstrating the role of access to sucrose resources in enhancing reproductive success of parasitoids.

In chapter 3, we conducted a greenhouse experiment to assess the suitability of floral nectar on the longevity, egg load, and egg volume of parasitoid females. We chose buckwheat (*Fagopyrum esculentum*), lacy phacelia (*Phacelia tanacetifolia*), deerhorn

clarkia (*Clarkia pulchella*), canola (*Brassica napus*), and safflower (*Carthamus tinctorius*) based on their use in pollinator enhancement and as non-cereal crop in Montana. The results of this study showed that *B. cephi* increased longevity with access to buckwheat and safflower flowers, and egg load and egg volume increased with access to buckwheat and deerhorn clarkia flowers. Also, the egg load of *B. lissogaster* was increased with access to deerhorn clarkia flowers. It is possible that sucrose dominant flowers, such as buckwheat, may provide the greatest benefit to parasitoids. However, other flowering species with similar nectar composition should be evaluated to validate this. This is valuable initial information that informs on selection of floral species that are suitable for enhancing effectiveness of parasitoids. Future studies should also consider flower morphology, which can play an important role in nectar accessibility, and therefore selection of suitable floral resources to habitat management.

One of the objectives of this study was to identify plant species that were both beneficial to the parasitoids, and practical for cropping. Although buckwheat seems to be the best option to enhance effectiveness of *B. cephi* females, this species is excluded from conservation plantings adjacent to wheat due to its potential to contaminate the wheat crop and the subsequent risk that buckwheat allergens pose to human health. In contrast, safflower and deerhorn clarkia may be of greater benefit for producers, as the cover crop species can provide an economic return, and the native species is historically widely-distributed and is now commonly included in seed mixtures for restoration of habitat for native pollinators. Planting these species will eliminate undesirable contamination of

Montana wheat by allergens that could occur when crops are grown adjacent to buckwheat.

Collectively, this research demonstrated the potential to enhance biological control by providing supplemental sucrose and nectar to wheat stem sawfly parasitoids. This information will be of considerable importance for improving the predictability of successful biological control of *C. cinctus*. However, the effect of sugar resources is not well understood and varies among both parasitoid and flowering plant species. Better understanding of the role of nutrients in reproductive biology is essential to determine how alternative food sources could contribute to the role each parasitoid species could occupy in the overall population dynamics of *C. cinctus*.

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