

Effects of sucrose supplementation and generation on life-history traits of *Bracon cephi* and *Bracon lissogaster*, parasitoids of the wheat stem sawfly

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Abstract. Knowledge of the life-history traits that influence the reproductive success of parasitoids could provide useful information to enhance their effectiveness as biological control agents. The wheat stem sawfly *Cephus cinctus* Norton (Hymenoptera: Cephidae) is a major pest of wheat in the Northern Great Plains of North America. The bivoltine, sympatric and specialist parasitoids *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae) are the only species known to attack *C. cinctus* in wheat. In the present study, we quantify the body size, longevity, egg load and egg volume of *B. cephi* and *B. lissogaster* aiming to test whether these life-history traits differ among adult females developing from overwintering and summer generation larvae. We also investigate the effect of sucrose supplementation on the same reproductive parameters. The results obtained show no differences between life-history traits of *B. cephi* developing from the overwintering and summer generations. By contrast, the egg load of *B. lissogaster* is significantly different between generations, with overwintered females producing 1.2-fold more eggs than summer individuals. Sucrose feeding has a strong positive effect on life-history traits of both parasitoid species and generations. The longevity of sucrose-fed females of *B. cephi* is increased three-fold, whereas the survival of *B. lissogaster* is increased almost nine-fold. Females of *B. cephi* treated with sucrose have four-fold more mature eggs, whereas the egg load of *B. lissogaster* is increased 1.15- to 1.25-fold with sugar feeding. Only *B. cephi* females increase egg volume with sucrose. The present study provides valuable insights on the life-history and nutritional requirements of these two important parasitoid species.

Key words. Biological control, bivoltine, body size, congeneric, egg resorption, sympatric, synovigenic.

Introduction

Food has a major impact on life-history traits of insects. The quantity and quality of food consumed by the larva can influence its growth rate, development time, final body size and probability of survival (Boggs, 1981; Slansky, 1982; Honěk, 1993; Chown & Gaston, 2010; Douglas & Simpson, 2012). As adults, many insects depend on supplementary food sources to maximize their longevity and realized fecundity (Dadd, 1973;

Thompson, 1999; Winkler *et al.*, 2006; Thompson & Simpson, 2009; Harvey *et al.*, 2012; Panizzi & Parra, 2012; Nation Sr, 2015). This is especially relevant for the hymenopteran parasitoids that are used as biological control agents against agricultural pests. Although parasitoid larvae are carnivorous, developing in or on their arthropod host (Godfray, 1994; Balzan & Wäckers, 2013), the majority of adult parasitoids rely on carbohydrates as their main source energy (Rivero & Casas, 1999; Casas *et al.*, 2005; Heimpel & Jervis, 2005; Wäckers, 2005; Jervis *et al.*, 2008; Quicke, 2014; Benelli *et al.*, 2017). In the field, the most common sources of carbohydrates are plant-derived exudates, such as floral and extrafloral nectar (Wäckers, 2005). There is overwhelming evidence demonstrating that carbohydrates derived from floral nectar can increase

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parasitoid performance in agricultural systems (Stephens *et al.*, 1998; Tylianakis *et al.*, 2004; Heimpel & Jervis, 2005; Berndt *et al.*, 2006; Bianchi *et al.*, 2006; Simpson *et al.*, 2011; Tena *et al.*, 2015; Gurr *et al.*, 2017). Additionally, some parasitoid species require supplemental proteins to initiate or continue egg maturation, and adult females can obtain such resources by feeding on the host's haemolymph (Jervis & Kidd, 1986).

Bracon cephi (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae) are important parasitoid species in wheat cropping systems. They are the only species known to attack and successfully suppress damaging populations of *Cephus cinctus* Norton (Hymenoptera: Cephidae), which is the most destructive pest of wheat in the Northern Great Plains of North America (Morrill *et al.*, 1998; Runyon *et al.*, 2002; Weaver *et al.*, 2004, 2005; Beres *et al.*, 2011; Peterson *et al.*, 2011; Rand *et al.*, 2011; Cárcamo *et al.*, 2012; Buteler *et al.*, 2015; Adhikari *et al.*, 2018; Bekkerman & Weaver, 2018). Parasitism can kill up to 34% of *C. cinctus* larvae in a cohort and 12% of this mortality is irreplaceable, meaning that the mortality caused by *B. cephi* or *B. lissogaster* cannot be replaced by another mortality factor (Buteler *et al.*, 2015). However, the occurrence and abundance of these parasitoid species vary greatly among wheat fields and regions, compromising their effectiveness in the reliable management of this pest (Morrill *et al.*, 1998; Cárcamo *et al.*, 2012; Davis, 2013; Adhikari *et al.*, 2018).

The present study aims to investigate the effects of sucrose on key life-history traits of *B. cephi* and *B. lissogaster*. Such information contributes to the initial understanding of carbohydrate nutrition in these species, and potentially others, that are not known to host feed. Moreover, the results obtained can contribute to the development of a more effective biological control program for *C. cinctus*. Both parasitoid species are likely to benefit from sugar supplementation. Early records report *B. cephi* individuals foraging flowers and consuming nectar in the field (Nelson & Farstad, 1953), whereas *B. lissogaster* adults are reared using honey and sugar solution to increase longevity (Somsen & Luginbill Jr, 1956). Despite that, little is known about the potential of carbohydrates on the reproductive traits of *B. cephi* and *B. lissogaster*.

Bracon cephi and *B. lissogaster* are sympatric, specialists, sharing very similar biology. They are both ectoparasitoids and idiobionts, meaning that females paralyze their hosts prior to oviposition (Nelson & Farstad, 1953; Somsen & Luginbill Jr, 1956). *Bracon cephi* is solitary, with only one egg being deposited per host (Nelson & Farstad, 1953), whereas *B. lissogaster* is gregarious and females can lay up to four eggs per host (Somsen & Luginbill Jr, 1956). The larva completes development in approximately 10 days and subsequently spins a cylindrical cocoon that is firmly held inside the wheat stem (Nelson & Farstad, 1953). They have two generations per year, (Cridle, 1923; Nelson & Farstad, 1953; Morrill, 1997). However, the success of the second generation depends on host plant phenology, as well as how late in the season the first-generation females continue to oviposit. For example, eggs deposited in June or July will hatch, feed on the larval host, pupate and emerge as adults later in the season, whereas the progeny of eggs laid in July or August overwinter as larvae, and they will

only pupate and emerge as adults in the subsequent season (Holmes *et al.*, 1963).

Unlike their host *C. cinctus*, which overwinters below the soil surface, most parasitoid larvae overwinter above ground in standing stems and are exposed to unfavourable winter conditions (Holmes *et al.*, 1963). Therefore, the ability to withstand low temperatures is critical for their survival. For example, *B. cephi* larvae are known to accumulate great concentrations of the cryoprotectant glycerol, equivalent to 25% of their body mass, to avoid freezing or allow survival even if frozen (Salt, 1959). However, such an investment can also be costly. Because mature larvae are inactive and do not feed during diapause, energy reserves are limited and investment in diapause may trade-off against adult fitness. Several studies report the costs of diapause by comparing life-history traits between post-diapause and non-diapause adults, finding that post-diapause individuals have a smaller body size (Sadakiyo & Ishihara, 2012), as well as decreased longevity (Larson & Duan, 2016) and fecundity (Ishihara & Shimada, 1994; Ellers & van Alphen, 2002; Sadakiyo & Ishihara, 2012; Larson & Duan, 2016).

Therefore, the present study quantifies the body size, longevity, egg load and egg volume of *B. cephi* and *B. lissogaster* to test whether these key life-history traits differ among adult females developing from the overwintering and summer generations. Moreover, we investigate the effect of sucrose supplementation on those traits that are known to directly influence reproductive success of parasitoids.

Materials and methods

Parasitoids

The overwintering generation of *B. cephi* and *B. lissogaster* was collected as pre-pupae from wheat stubble that was heavily infested by *C. cinctus* in wheat fields near Amsterdam, Montana, USA (May 2015 and June 2016, 45°45'32.4"N, 111° 23'49.2"W). Wheat stem samples were dissected and overwintered individuals in cocoons were collected, stored in plastic bags (16.5 × 14.9 cm) and kept in cold storage (0–4 °C) for 1–3 months to delay adult emergence. Afterwards, cocoons were placed into glass jars (236 mL) and stored in a growth chamber (E30B; Percival Scientific, Perry, Iowa) under controlled conditions (LD 12 : 12 h photoperiod at 25 ± 2 °C and 40–60% relative humidity) until the adults emerged. Summer generation parasitoids were reared from ripened winter wheat samples containing parasitoid cocoons. The samples were collected throughout Montana, U.S.A., 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 black plastic trash barrels (121 L; 56 × 63 × 71 cm) with lids. Barrel lids had a hole (diameter 11 cm) cut in the centre where cones made of clear laminating sheets were glued with silicone sealant (GE5000; GE, Boston, Massachusetts). Clear plastic jars (500 mL; S-22855; Uline, Pleasant Prairie, Wisconsin) were placed over the cones to

capture emerging adult parasitoids. Emergence barrels were kept at room temperature ($25 \pm 5^\circ\text{C}$) until the emergence of parasitoids. Jars and barrels were checked daily, and emerged females were individually placed inside plastic Petri dishes for immediate use in experiments. Samples sizes were unequal because of variation in population density among sites. Parasitoids were identified using the morphological characters described in Runyon *et al.* (2001).

Longevity

To test the effect of carbohydrate supplementation on longevity of both generations of *B. cephi* and *B. lissogaster*, newly emerged adult females were held individually in plastic Petri dishes. Then, individuals were randomly assigned to one of the two treatments: control and sucrose (*B. cephi*: overwintering, $n = 28$ and summer $n = 27$; *B. lissogaster*: overwintering, $n = 23$ and summer $n = 14$). Sucrose was chosen for being the most common carbohydrate in floral nectar (Nicolson & Thornburg, 2007; Wäckers *et al.*, 2008). We offered a 30% (w/v) of sucrose solution through a soaked piece of dental cotton roll (1×1 cm, 0.1 g). At this concentration, sucrose has been shown to promote high phagostimulation (feeding response) in parasitoids (Wäckers, 1999). For the control treatment, water was offered as described for sucrose. Petri dishes were placed inside a growth chamber under an LD 12 : 12 h photoperiod at $25 \pm 2^\circ\text{C}$ and 40–60% relative humidity. 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 micrometre (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 & Mills, 2003; Ellers & Jervis, 2003; Saeki & 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. Before the experiments, females were randomly assigned to three age categories: 2, 6 and 10 days old. Age categories were then subdivided in two treatment groups: control and sucrose (*B. cephi*: overwintering, $n = 60$ and summer $n = 23$; *B. lissogaster*: overwintering, $n = 61$ and summer $n = 76$). Water and 30% (w/v) sucrose solution were offered as described above. Petri dishes were kept in controlled conditions (LD 12 : 12 h photoperiod at $25 \pm 2^\circ\text{C}$ and 40–60% relative humidity) for either 2, 6 or 10 days, in accordance with the assigned age categories. Females were freeze killed ($-32 \pm 1^\circ\text{C}$) 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; eight parts 95% ethyl alcohol, three parts formalin, one 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, Germany) at $2\times$ magnification. Eggs were removed from the ovaries and mature eggs counted. Only curved sausage shape eggs, tapering towards 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 DINO-CAPTURE, version 2.0 (Dino-Lite). Volume (V) in μm^3 of each egg was estimated as $V = (\pi \cdot r^2)(L - 2r) + (4/3)(\pi \cdot r^3)$, where L is length, D is 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 (The R Project for Statistical Computing, Austria) in conjunction with the integrated development environment RSTUDIO, version 1.0.136 (RStudio Team 2016). The effect to sucrose feeding on the longevity of parasitoid females was analyzed using log-rank test ('survival' package in R) (Therneau & Grambsch, 2000). We used generalized linear models and logarithmic link function in the 'MASS' package (Venables & Ripley, 2002) to determine the effect of age, sucrose, and body size on the egg load of females from overwintering and summer generations. 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 regression analyses to describe the relationship between egg load and body size of females. To analyze the effect of age, sucrose and body size on egg volume of both generation adult females of *B. cephi* and *B. lissogaster*, we used a linear mixed model ('lme4' package) (Bates *et al.*, 2015) treating individual parasitoids as a random factor. For these data, the assumptions of normality and homoscedasticity were met. Probability values were calculated using log-likelihood ratio tests and the analysis of variance function in the 'car' package (Fox & Weisberg, 2018). Models were simplified through stepwise deletion of terms using Akaike's information criterion.

Results

Longevity

We found no differences in longevity between adults from the 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*, $P = 0.22$). By contrast, sucrose supplementation 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). 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. 1B).

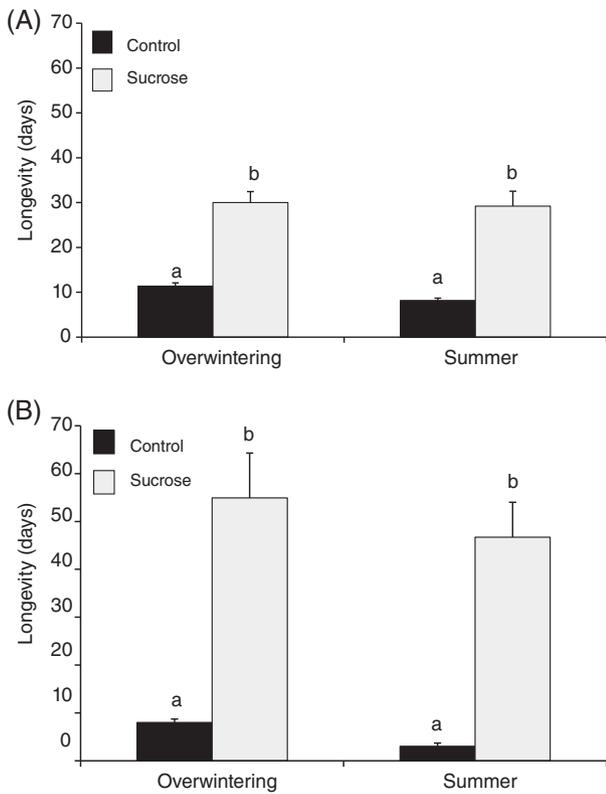


Fig. 1. (A) Longevity (mean \pm SE) of *Bracon cephi* and (B) *Bracon lissogaster* treated with water (control) or sucrose solution. Treatments were offered *ad libitum* to parasitoid females until death. Bars followed with the same lowercase letter indicate no significant differences ($P > 0.05$) based on statistical analysis using log-rank tests.

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 ($P = 0.09$) (Fig. 2A) and body size ($P = 0.09$) (Fig. 3A, B) on the egg load of *B. cephi*. However, the egg load of both generations significantly increased with sucrose feeding ($P < 0.0001$). Maximum egg load was reached after 6 days with an average four mature eggs (Fig. 2A). Control females also reached maximum egg load at age 6 days, although with only one egg (Fig. 2A). Most females did not survive up to 10 days. Therefore, no data are shown for this age (Fig. 2A).

In *B. lissogaster*, the egg load of females was significantly different between generations ($P < 0.05$) (Fig. 2B), positively correlated with body size ($P < 0.0001$) (Fig. 4A, B) and negatively correlated with age ($P < 0.0001$) (Fig. 2B). At day 10, females from the overwintering and summer generations had a significant smaller egg load compared with days 2 and 6 ($P < 0.001$) (Fig. 2B). However, at day 10, females of the summer generation had significantly fewer eggs than individuals from the overwintering generation ($P < 0.05$) (Fig. 2B). Because hosts were absent in the present 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*

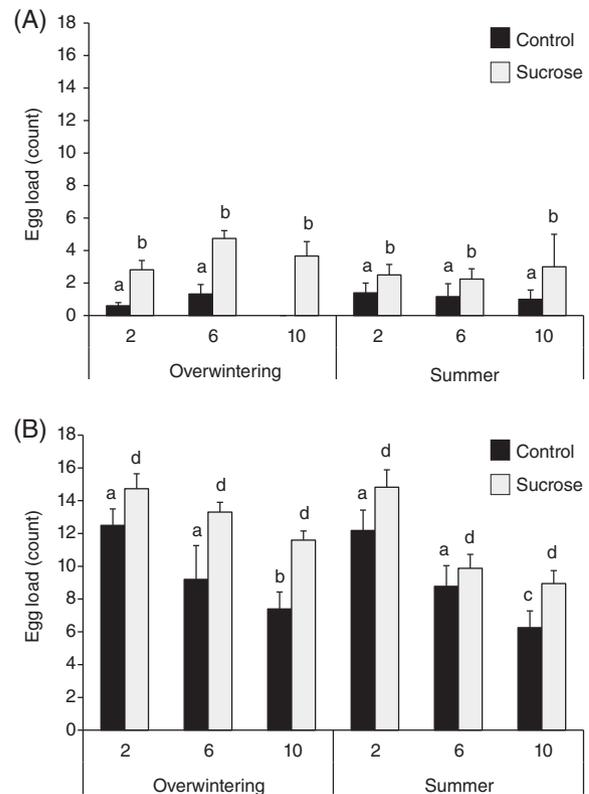


Fig. 2. (A) Mean \pm SE egg load of (A) *Bracon cephi* and (B) *Bracon lissogaster* females treated with water (control) or sucrose solution. Diets were offered *ad libitum* for 2, 6 and 10 days. Bars followed with the same lowercase letter indicate no significant differences ($P > 0.05$) based on statistical analysis using likelihood-ratio tests and generalized linear models.

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

Egg volume

The variables age (linear mixed model, $P = 0.36$) and body size ($P = 0.09$) (data not shown) did not affect egg volume of females from the overwintering and summer generations of *B. cephi*. By contrast, sucrose feeding significantly affected egg volume in this species ($P < 0.0001$), with an estimated mean \pm SE increase of $0.0089 \pm 0.0015 \mu\text{m}^3$ compared with the control (Fig. 5A). For *B. lissogaster* none of these variables affected egg volume of overwintering and summer adult females (age, $P = 0.09$; body size, $P = 0.28$; sucrose, $P = 0.1$) (Fig. 5B).

Discussion

The results obtained in the present study show no differences in body size, longevity, egg load and egg volume between

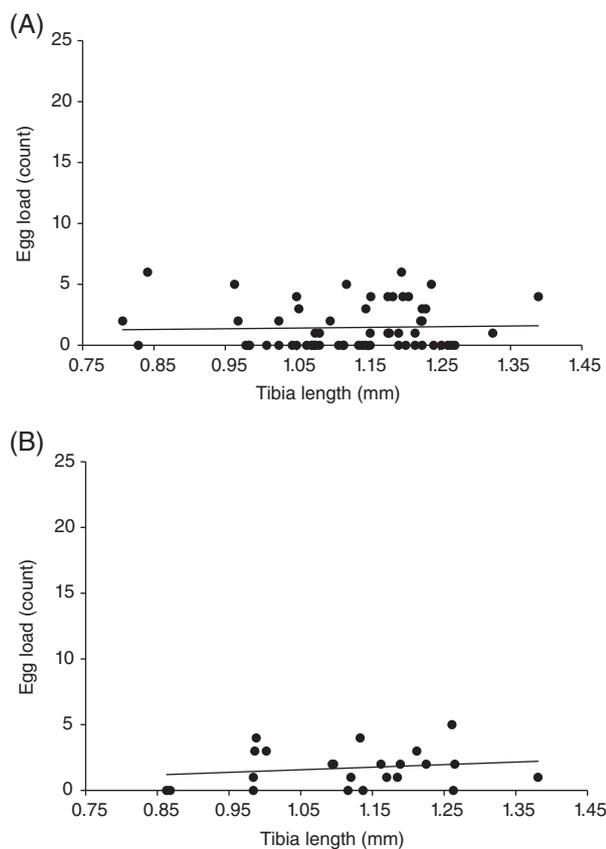


Fig. 3. Scatterplot of the relationship between egg load and body size in (A) overwintered and (B) summer females of *Bracon cephi* ($P = 0.09$).

overwintering and summer generations of *B. cephi*. The results are similar for *B. lissogaster* adult females; however, we find that their egg load is significantly different between generations. Additionally, we find a strong positive effect of sucrose supplementation on the reproductive traits of both parasitoid species and generations. Our findings highlight the contrasting life histories of these two sympatric, specialist parasitoids. These differences, together with the benefit from sucrose in adult parasitoid nutrition, may have important implications for the successful biological control of *C. cinctus*.

Carbohydrates are the primary source of energy to fuel metabolic maintenance in parasitoids (Hausmann *et al.*, 2005; Jervis *et al.*, 2008; Wäckers *et al.*, 2008) and, as expected, sucrose has a major effect on the longevity of both *B. cephi* and *B. lissogaster*. We also find a significant increase in egg load when sucrose is provided (Fig. 2A, B). However, the effect of carbohydrates on the egg load of *B. cephi* and *B. lissogaster* is more likely to be indirect. Oogenesis is mostly dependent on lipid and protein reserves (Rivero & Casas, 1999; Jervis *et al.*, 2008). However, such resources can also support somatic maintenance, especially when adult females spend long periods of time without feeding and when sugar levels decrease below a certain threshold (Casas *et al.*, 2005). Due to the importance of lipids and proteins for egg production, the consumption of these nutrients for survival can be detrimental to reproduction

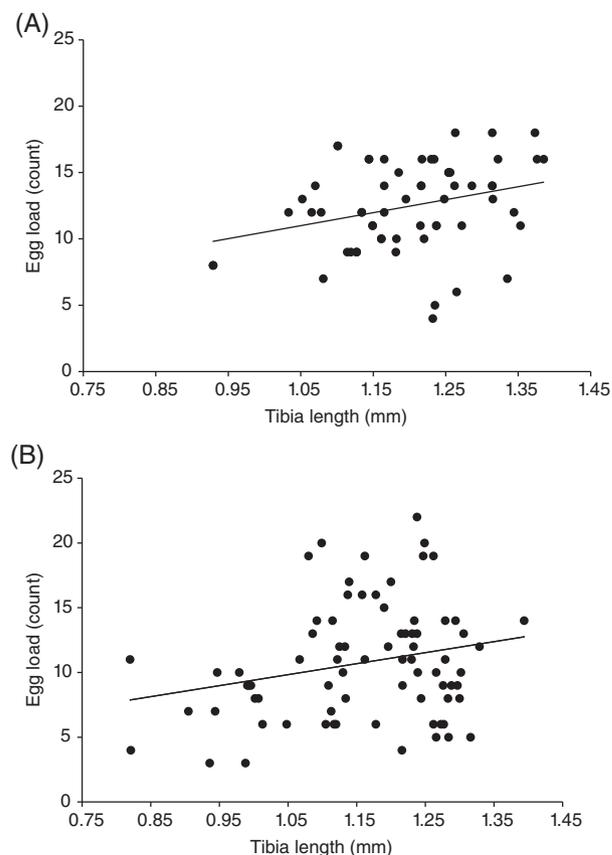


Fig. 4. Scatterplot of the relationship between egg load and body size in (A) overwintered and (B) summer females of *Bracon lissogaster* ($P < 0.0001$).

(Casas *et al.*, 2005). Thus, more than supporting the energetic demands of parasitoids, sucrose provision could play an important role that enables females to invest more lipids and proteins towards egg production. However, the specifics of nutrient allocation into egg manufacture in *B. cephi* and *B. lissogaster* still remain to be investigated.

Sucrose feeding also had a strong positive effect on egg volume of *B. cephi* (Fig. 5A). Egg size is considered to be a good predictor of fitness (Roff, 1992; Mousseau & Fox, 1998; Fox & Czesak, 2000). The quantity of nutrients allocated to eggs can determine the amount of resources initially available for the offspring, as well as their body size (Larsson, 1990; Bernardo, 1996; Budriené *et al.*, 2013). Thus, by investing more in each egg, females might influence growth and survival probability of their progeny (Roff, 1992; Mousseau & Fox, 1998; Fox & Czesak, 2000; Allen *et al.*, 2007; Muller *et al.*, 2017). In parasitoids, increased investment in egg size is shown to correlate with female body size (O'Neill & Skinner, 1990), age (Giron & Casas, 2003; Muller *et al.*, 2017) and nutritional status (Fox & Czesak, 2000; Cicero *et al.*, 2012). However, in the present study, we find no effect of body size and age on egg volume of *B. cephi*. As discussed above, sucrose could be indirectly influencing the amount of nutrients invested per egg by decreasing the use of proteins that are highly correlated

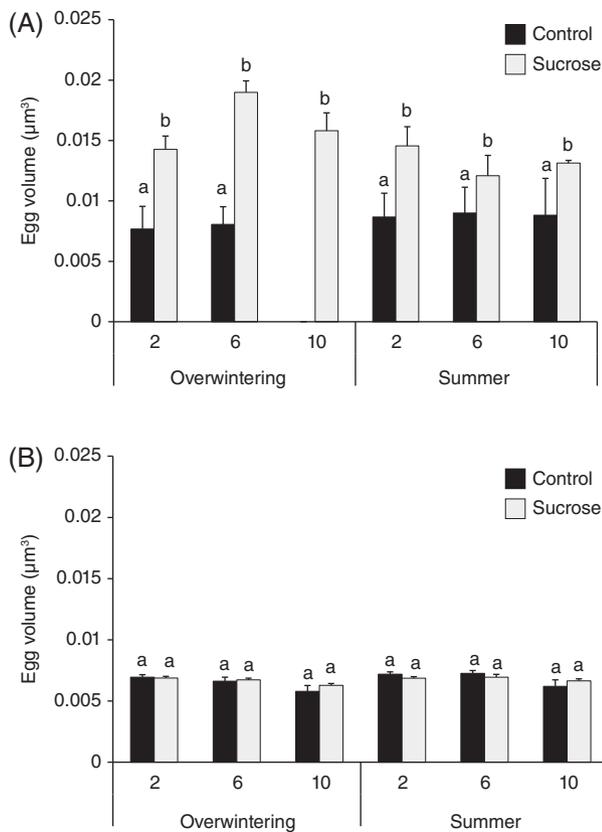


Fig. 5. Mean \pm SE of estimated egg volume (μm^3) of (A) *Bracon cephi* and (B) *Bracon lissogaster* females treated with water (control) or sucrose solution. Diets were offered *ad libitum* over 2, 6 and 10 days. Bars followed with the lowercase same letter indicate no significant differences ($P > 0.05$) based on statistical analysis using linear mixed models.

with egg size (Giron & Casas, 2003). Nevertheless, the nutrient composition of *B. cephi* and *B. lissogaster* eggs is still unknown and quality of resources allocated into eggs can be ecologically and evolutionary more important than variation in egg size (Parker & Begon, 1986; Bernardo, 1996; Fox & Czesak, 2000).

Although we find significant differences in egg load between generations of *B. lissogaster*, these results may be a result of the strong effect of age in this species. The egg load of females from both generations significantly decreases as they age (Fig. 2B). However, at 10 days old, summer females carry even fewer eggs than overwintered individuals (Fig. 2B). These results indicate that egg resorption occurs in this species and summer females appear to resorb more eggs later in life compared with overwintered individuals. Egg resorption is a common reproductive strategy among parasitoids (Bell & Bohm, 1975; Jarvis *et al.*, 2001) and it can be a means of eliminating defective oocytes, maintaining a constant supply of newly mature eggs and/or providing energy in periods of nutrient stress (King & Richards, 1968; Bell & Bohm, 1975; Collier, 1995; Rivero-Lynch & Godfray, 1997; Rosenheim *et al.*, 2000). By resorbing eggs, females can control the timing of the next energy gain despite the availability of food resources (Richard &

Casas, 2009). However, when food is available, egg resorption may occur at a slower rate, or not even occur (Collier, 1995; Heimpel & Rosenheim, 1995; Heimpel *et al.*, 1997; Rosenheim *et al.*, 2000). Accordingly, our results show no differences in egg load with sucrose supplementation (Fig. 2B).

By contrast, our results show that *B. cephi* does not resorb eggs; hence egg maturation in this species may only occur when oviposition opportunities are available, or if individuals are not energy limited. This strategy appears to be adaptive because parasitoids emerge in synchrony with *C. cinctus* adults and only start laying eggs after an obligatory pre-oviposition period (Nelson & Farstad, 1953; Holmes *et al.*, 1963). Unlike *B. cephi*, *B. lissogaster* females emerge with a complement of already mature eggs. This strategy gives the advantage of maximizing the number of eggs ready for oviposition early on in life (Ellers *et al.*, 2000; Rosenheim *et al.*, 2000; Ellers & Jarvis, 2003; Jarvis & Ferns, 2004). However, early investment in reproduction may incur survival costs, and females could die before they are able to lay all their eggs (Sevenster *et al.*, 1998; Rosenheim, 2011; Dieckhoff *et al.*, 2014). Although *B. lissogaster* is capable of egg resorption, our results show that control females still die with mature eggs in the ovaries. Thus, the provision of carbohydrate resources may be essential for increasing the longevity, and therefore reproductive success of this species. We find no differences in body size between generations of *B. cephi* and *B. lissogaster*. However, the body size of *B. lissogaster* is positively correlated with egg load (Fig. 4A,B). Such a relationship is observed in several parasitoid species, and it appears to be associated with immature development and the amount of resources carried over from the larval stage (Honěk, 1993; Visser, 1994; Ellers *et al.*, 1998; Bezemer *et al.*, 2005; Henri & Van Veen, 2011; Mayhew, 2016). For example, *B. lissogaster* larvae can develop solitarily or gregariously (Somsen & Luginbill Jr, 1956). When more than two parasitoids are feeding on the same host, the development time is reduced, most likely because of the decreased availability of food (Somsen & Luginbill Jr, 1956). Even under crowded conditions, *B. lissogaster* larvae develop normally and completely, although they are smaller than those that feed solitarily (Somsen & Luginbill Jr, 1956). This suggests that larger females may have access to more resources; thus, they store more energy reserves and produce more eggs than smaller conspecifics. However, the positive effect of body size on the increased egg load of *B. lissogaster* females may be of limited importance if many factors are contributing to parasitoid mortality in the field. Therefore, the use of cultural practices that support conservation of parasitoids is essential for increasing 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 the mortality of *Bracon* spp. overwintering above ground in standing stems, which would otherwise be killed during such operations (Runyon *et al.*, 2002; Meers, 2005; Beres *et al.*, 2011; Adhikari *et al.*, 2018). In conclusion, the present study highlights the differences in reproductive strategies between two specialist congeneric parasitoids that are almost identical in appearance and fully sympatric. We also provide insights on the nutritional requirements of these two important parasitoid species. However, these effects remain to be investigated in the field, and more studies

are encouraged to explore how other sources of food, such as floral nectar, can benefit the reproductive success of *B. cephi* and *B. lissogaster*.

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