Parasitism and the demography of wheat stem sawfly larvae, *Cephus cinctus*

**Robert K. D. Peterson · Micaela Buteler ·
David K. Weaver · Tulio B. Macedo · Zhitan Sun ·
Oscar Gerardo Perez · Godshen R. Pallipparambil**

Abstract Previous research has suggested that insect herbivores in protected environments have higher mortalities from biotic factors such as parasitism compared to herbivores in less protected situations, although overall mortalities in protected environments are often lower. However, this has not been examined using life table approaches. In this study, we used demographic methods to characterize the mortality dynamics of parasitism for pre-diapause wheat stem sawfly larvae, *Cephus cintus* Norton (Hymenoptera: Cephidae), a stem-mining wheat pest. Larvae were intensively sampled from commercial wheat fields at two locations in Montana, USA from 2005 through 2008. The feeding larvae present in the summer succumbed to only two mortality categories: parasitism and unknown factors. In Conrad, a location with relatively high densities of the parasitoids, mortality by parasitism was largely irreplaceable. In contrast, in Amsterdam, where parasitism did not occur to any appreciable degree, overall mortality remained relatively low.

Introduction

Analytic techniques to estimate mortality within multiple decrement life tables, such as estimating the risks of insect death in the presence or absence of multiple causes, are important tools for population and applied ecology (Carey 1989, 1993). Peterson et al. (2009) concluded that it is not possible to estimate the effect of any mortality factor without considering its interaction with competing mortality factors. They constructed multiple decrement life tables from 73 insect life tables published between 1954 and 2004 and found that irreplaceable mortality (the portion of mortality that cannot be replaced by another cause) from pathogens, predators, and parasitoids was significantly lower than the mean irreplaceable mortality from all factors other than natural enemies. From this research, they suggested that the degree of environmental protection and stability most likely increases the magnitude of the irreplaceable mortality from natural enemies.

In addition to Peterson et al. (2009), other researchers have suggested that insect herbivores in protected environments, such as physical refuges, have higher mortalities due to specific factors such as parasitism compared to herbivores in unprotected

R. K. D. Peterson (✉) · M. Buteler · D. K. Weaver ·
T. B. Macedo · Z. Sun · O. G. Perez ·
G. R. Pallipparambil
Montana State University, Bozeman, USA
e-mail: bpeterson@montana.edu

situations, although overall mortalities in protected environments are often lower (Cornell and Hawkins 1995; Hawkins 1994; Hawkins et al. 1999; Price 1991; Price and Pschorn-Walcher 1988; Southwood and Comins 1976). To our knowledge, however, this phenomenon has not been examined using demographic approaches. Moreover, mortality dynamics using multiple decrement life tables have never been characterized for an insect in a physical refuge, such as a stem-mining species.

The wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), is well suited for examining mortality dynamics. The WSS is univoltine and its life cycle is synchronized with the physiological development of the host plants, infesting both spring and winter wheat, *Triticum aestivum* L. (Morrill and Kushnak 1996). Adults emerge from obligate, overwinter diapause in the wheat stubble which remains in the field following harvest. Adult males generally emerge first and remain near field edges where most mating occurs. However, mating is not necessary for production of viable eggs as females can control the sex of their offspring by laying either a fertilized diploid female egg or an unfertilized haploid male egg (Holmes 1982; Morrill et al. 2000). The average lifespan of the adults is 5–8 days depending on climatic conditions and available moisture (Criddle 1923).

Plants are vulnerable to attack from initiation of stem elongation through anthesis (Morrill and Kushnak 1999). A female may lay as many as 50 eggs, and several eggs can be deposited in each stem, particularly under high population densities (Buteler et al. 2009). Other females may lay eggs in the same stem, but only one larva will survive due to cannibalism within the wheat stem (Wallace and McNeal 1966). The eggs take approximately 5–8 days to hatch and the larvae develop within the wheat stems and feed on parenchyma and vascular tissues for a month or longer (Ainslie 1929). Larval development is completed after four or five larval stadia, depending on the host species (Farstad 1940). As the host plant starts to senesce, the larva moves down the stem, cuts a v-shaped notch around the stem interior, and plugs the stem below the notch with frass and plant materials (Holmes 1975). Larvae overwinter in diapause inside these plugged cut stems within the wheat residue for 8–9 months until pupation occurs the following spring. Pupal development lasts from 7

to 16 days before adult emergence commences the next life cycle (Church 1955; Holmes 1975).

Two congeneric parasitoids, the larval idiobionts, *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae), can suppress WSS populations in wheat in Montana, USA (Morrill 1998; Runyon et al. 2002; Weaver et al. 2005). These solitary ectoparasitoids attack WSS larvae feeding within various hosts, including feral grasses and cultivated wheat, by inserting their ovipositor through the stem wall to sting and paralyze the endophagous late-instars. Parasitism varies greatly between fields mainly due to environmental conditions, the date of crop harvest, and WSS abundance (Holmes et al. 1963). The parasitoids are bivoltine (Nelson and Farstad 1953) and the relative success of the second generation in wheat fields has been viewed as a limiting factor in population growth, especially when drought speeds crop maturity (Holmes et al. 1963). The biology of *B. lissogaster* is distinct because multiple offspring can arise from a single host while only one adult is produced per WSS paralyzed by *B. cephi* (Somsen and Luginbill 1956).

Because WSS females oviposit in stems and the egg, larval and pupal stages are entirely spent within stems, recruitment of individuals and mortality can be precisely tracked. Further, the individuals are relatively protected within the stems, enhancing the ability to estimate the magnitude of mortality from the various mortality factors. Finally, because the stems protect the individuals from many different potential mortality factors, such as the predation that is typical to externally feeding immature, we can examine in detail the mortality from parasitoids and test a hypothesis that the irreplaceable mortality from the parasitoids is high when they are present.

Materials and methods

Wheat stems and larvae were intensively sampled from commercial wheat fields at two locations between 2005 and 2008. One of the fields, sampled in 2005, 2007 and 2008, was located between Pendroy and Conrad in Pondera County in north-central Montana, USA (48°8.00′ N, 112°6.68′ W). The other field, sampled in 2005, 2006 and 2007, was near Amsterdam in Gallatin County in southwest Montana (45°45.025′ N, 111°25.190′ W). The sites
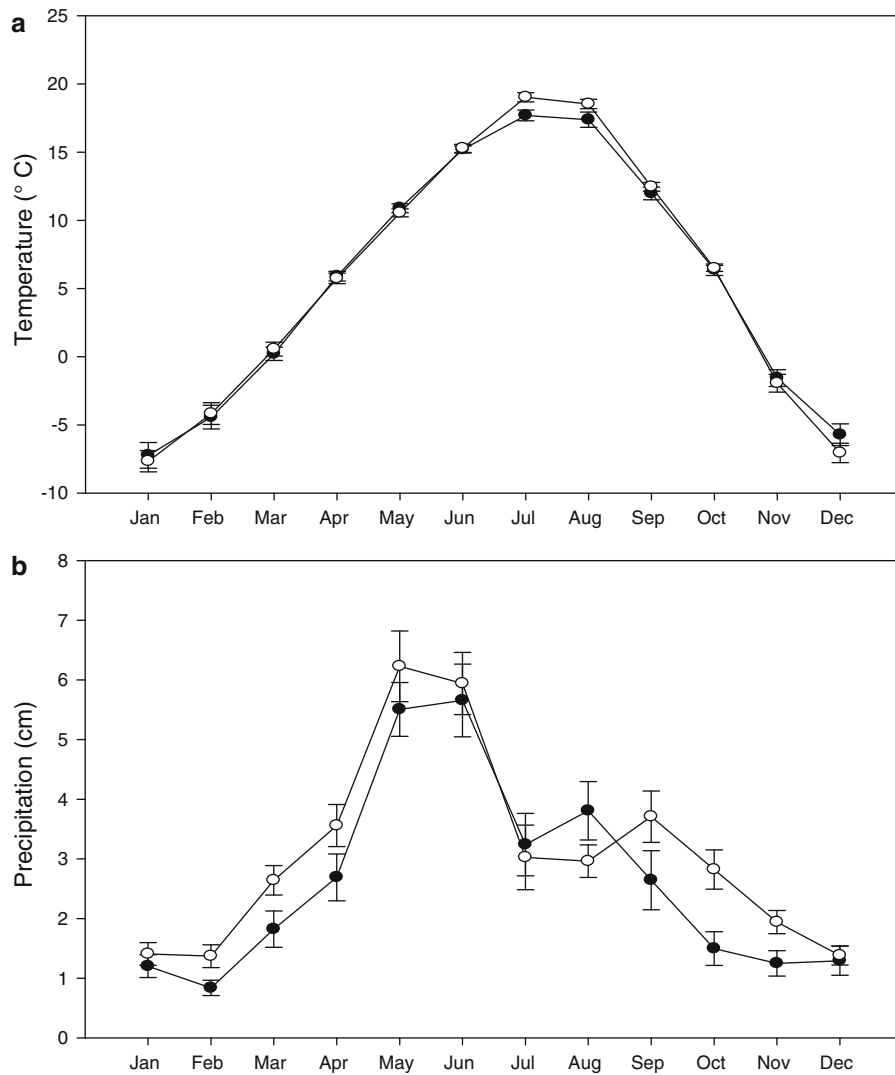
Fig. 1 Plots of 30 year average monthly temperature (**a**) and monthly precipitation (**b**) for weather stations near the Amsterdam (line with open circle) and Conrad (line with filled circle) experimental sites. Data are means (±SE) obtained from daily records collected from 1971–2000 at locations within 20 km of each site

were chosen because the Conrad area has a recent history of high WSS parasitism and the Amsterdam area does not. Both sites were conventional rainfed monocultures of hollow-stem spring or winter wheat in which the growers practice alternate-year fallowing of cropland to replenish soil moisture. However, there are key differences between the areas surrounding the sites. Although the 30 year average temperature is almost identical for each month, precipitation is much greater consistently from September through June (Fig. 1) for Gallatin County (USNOAA 2002). Pondera County has 121,850 hectares of cropland of which 86% is devoted to cereal production, while Gallatin County has 63,050 hectares of cropland of which 49% is devoted to cereal production. In both counties, about 27,520 hectares of cropland is irrigated, with 62% of irrigated crop production being cereals in Pondera County, but only 35% of irrigated cropland is grown to cereals (USDA-NASS 2009). From 2005 to 2008, spring wheat yield in Pondera County was 63% of the yield for Gallatin County, while for 2005–2007 winter wheat yield in Pondera County was 90% of that for Gallatin County (USDA-NASS 2011).

In Conrad, spring wheat cv. Reeder (study years 2005, 2008) and winter wheat cv. Neeley (study year 2007) were planted. In Amsterdam, spring wheat cv. McNeal (study year 2005), and Cheyenne (study year 2006), and winter wheat cvs. Falcon and Pryor (study year 2007) were planted. All cultivars were hollow-stem (susceptible) varieties.

At each location, 3×30 m plots were established within a strip of crop of approximately 200×1000 m. In Amsterdam 2005, three plots were established on the field margin and three plots were 33 m from the edge of the field and separated by 300 m. Plant samples containing WSS larvae were collected weekly from when ovipositing females were first observed in the field through harvest. At the Conrad location, two plots were placed on the field margin and two plots were placed 33 m from the edge of the field. Five plants, consisting of two to five stems each, were collected weekly from each plot in 2005 and ten plants were collected during the rest of the study. Other than as stated for 2005, a sample unit consisted of main stems and tillers of ten plants was collected randomly from each plot.

The samples were taken to the laboratory and processed by dissecting each stem and characterizing the stage of the larva, whether a host was alive or dead, and mortality was categorized. Determining the larval instars of field collected WSS for direct comparison is difficult due to variable larval sizes among microenvironments and cultivars. This is because WSS larval size is constrained by the host it occupies like many cryptic species developing within their hosts (Morrill et al. 2000; Morrill and Weaver 2000). We have observed that as the larvae grow bigger, the area of the stem that has been bored or eaten increases. Therefore, we considered the number of internodes bored within the stem as an indirect indicator of larval size and placed the larvae into one of three size classes (early, middle, or late) which also corresponded to sequential time periods during the summer development period. All data collected encompassed only two mortality categories (parasitism and unknown factors) and the individuals were followed from egg hatch to wheat harvest (last instar entering the pre-pupal stage for diapause). The parasitism was from two congeneric host-specific ectoparasitoids: *Bracon cephi* and *B. lissogaster*. Given that there are no characters available to distinguish between the two species of parasitoids as immatures (Runyon et al. 2002; Weaver et al.

2005), the level of parasitism reported was pooled for the two braconid species for all analyses. The designation of "unknown factors" refers to the observation of a dead larva, but the cause of death could not be readily determined. Most of the larvae in the unknown death category, however, were likely the result of abiotic factors such as heat stress because there were no symptoms associated with pathogens (Wenda-Piesik et al. 2009) nor were there any visible signs of parasitism.

Calculation techniques for multiple decrement life tables used the methods described by Carey (1993), Peterson et al. (2009) and Davis et al. (2011). We used an elimination-of-cause method as part of the spreadsheet program M-DEC (Davis et al. 2011) to examine combinations of causes of death in relationship to the absence of other causes and to frame each factor in terms of irreplaceable mortality. Variables are defined as: x the life stage index, l_x the number of individuals alive at each x, k_x the number at the beginning of each x, d_x the total number of deaths in each stage, al_x the fraction of the cohort living at the beginning of the stage (starting at 1.0 for the first stage and calculated by $al_{x-1} - ad_{x-1}$), $ad_{i\,x}$ fraction of deaths attributable to one cause, ad_x fractions of all deaths from all causes ($ad_{1x} + ad_{2x} + \ldots. + ad_{5x}$), and, aq_x stage-specific probability of death within that stage calculated by the sum of the probability of dying from all listed causes (d_x/k_x).

An algorithm represented by a quadratic formula for irreplaceable mortality was used to generate mortality solutions for independent mortality factors in the absence of all other factors. Briefly, elimination-of-cause analysis relies on the probability of surviving each source of mortality (p_x) and its complement $(1 - q_x)$ where $(1 - q_1)\,x \ldots x\,(1 - q_n)$ is the chance of jointly surviving a set of mortality factors and its complement, $1 - [(1 - q_1)\,x \ldots x\,(1 - q_n)]$, is the chance of jointly dying from a set of mortality factors. To estimate mortality in the absence of one or more factors, two simultaneous equations with two unknowns must be used. For example, by expressing q_1 (e.g., parasitism) in terms of q_2 (e.g., all other mortality factors), D_1 and D_2 (the fraction of all individuals observed that died of cause 1 and 2), this yields the quadratic equation $aq_2^2 + bq_2 + c = 0$, where $a = D_1$, $b = -(D_1 + D_2)$ and $c = D_2(D_1 + D_2)$. The value of q_2 can be found by substituting a, b, and c into the quadratic formula (Davis et al. 2011).

Results

A total of 3,328 larvae were collected over all locations and years. At the Amsterdam location, 494, 503, and 617 larvae were collected in 2005, 2006, and 2007, respectively. At Conrad, 475, 963, and 276 larvae were collected in 2005, 2007, and 2008, respectively. In 2005, when only five plants were collected at each sampling plot, the coefficient of variation among samples averaged 65% in the interior plots and 19% at the edge. The higher coefficient of variation in the interior samples is because a few samples contained no larvae, which can happen primarily when lower population levels result in a distribution where most larvae are found on the field periphery (Nansen et al. 2005; Weaver et al. 2005). For the remainder of the study, each sample consisted of ten plants and the coefficient of variation among samples within a date and site averaged 19.8% for the edge and 23.1% for the interior.

Multiple decrement life tables were constructed for each location and year (Tables 1 and 2). The feeding larvae present in the summer succumbed to only two mortality categories: parasitism and unknown factors. Although overwintering larvae and the pupae present in the spring also experience mortality from fungi, bacteria, viruses, and predation, the occurrence of only two mortality types for active larvae in the summer is most likely the result of the relatively protected environment provided by the endophagous feeding habit within the stem.

Data in the tables represent the probability of death from the specified causes in the presence of all causes by stage and over all stages. For example, the life table data for Conrad in 2005 reveal that there was a 43% probability of WSS dying during the third larval category. The probability of dying in the third larval category from parasitism in the presence of the unknown mortality factors was 16%. The total mortality was 43% from parasitism and 25% from unknown factors (Table 1).

The data reveal that percent mortality varied by location and year. More important, the data suggest that in Conrad, a location with relatively high densities of the parasitoids, mortality by parasitism was irreplaceable (Table 3). This trend was observed for all three years of the study and the irreplaceable mortality from parasitism was similar across years, ranging from 27% to 43%. Interestingly, for spring wheat the mortality of the youngest larval category from parasitism was greater than for winter wheat. Winter wheat is consistently available for infestation by WSS earlier in the season, so parasitoids ovipositing on larvae in winter wheat are likely to parasitize larger larvae than spring wheat. This is linked to an obligate pre-oviposition interval. Nelson and Farstad (1953) reported a pre-ovipositional period of 21 days for *B. cephi*, although a later paper based on field data for this species indicated oviposition may begin 12–18 days after adult emergence (Holmes et al. 1963). Despite differences in the stage of the parasitized larvae across years, which could be due to differences in the size of WSS larvae at the time parasitism occurs, the total irreplaceable mortality due to parasitism was similar across years in Conrad. This suggests that when parasitoids are present, parasitism represents an important mortality factor because this source of mortality cannot be replaced by another factor. For example, in the presence of the unknown mortality factors, parasitism accounted for 43% mortality, but only 8% of that mortality would have been replaced by the unknown factors (43 − 35%) (Table 3). Without parasitism in 2005 in Conrad, mortality would have been reduced from 68% to 33% (68 − 35%). The unknown mortality factors would not have compensated appreciably for parasitoid mortality. In contrast, for the Amsterdam location, where parasitism was not present to any appreciable degree, overall mortality remained relatively low.

Mortality from parasitism did not vary greatly between years in each location. At the Conrad location from 2005 through 2008, mortality from parasitism in the presence of all factors ranged from 27% to 43%, and irreplaceable mortality from parasitism ranged from 22% to 35% (Table 3). At the Amsterdam location from 2005 through 2007, mortality from parasitism in the presence of all factors ranged from 0% to 2%, and irreplaceable mortality from parasitism ranged from 0% to 1%.

Total mortality and the mortality from the unknown factors did not vary considerably among years at the Conrad location, but varied appreciably at the Amsterdam location, especially in 2007 compared to 2005 and 2006 (Table 2). The recorded average maximum temperature in July and August 2007 in Amsterdam, when the larvae were developing inside the stems, was 8°C greater than the next hottest site-

Table 1 Multiple decrement life table for pre-diapause larvae of the wheat stem sawfly, *Cephus cinctus* Norton (Conrad, Montana, USA)

Year	Larval category, x	Crop type	Fraction dying, aq_x	Fraction living, al_x	Fraction of total dying, ad_x	Parasitism, aq_{1x}	Unknown, aq_{2x}
2005	Early	Spring wheat	0.244	1	0.244	0.173	0.071
	Middle		0.250	0.756	0.189	0.097	0.092
	Late		0.426	0.567	0.567	0.158	0.084
	Total				1	0.428	0.247
2007	Early	Winter wheat	0.087	1	0.087	0.011	0.077
	Middle		0.416	0.913	0.377	0.173	0.207
	Late		0.405	0.533	0.533	0.117	0.097
	Total				1	0.303	0.380
2008	Early	Spring wheat	0.388	1	0.388	0.060	0.328
	Middle		0.263	0.612	0.161	0.086	0.075
	Late		0.415	0.451	0.451	0.128	0.059
	Total				1	0.273	0.463

aq_x Fraction of deaths from all causes in stage x given that the individual is alive at the beginning of stage x, al_x fraction of survivors at stage x out of original cohort of al_1, ad_x fraction of deaths in stage x from all causes, aq_{ix} fraction of deaths from cause i in stage x in the presence of all other causes given that the individual is alive at the beginning of stage x

Table 2 Multiple decrement life table for pre-diapause larvae of the wheat stem sawfly, *Cephus cinctus* Norton (Amsterdam, Montana, USA)

Year	Larval category, x	Crop type	Fraction dying, aq_x	Fraction living, al_x	Fraction of total dying, ad_x	Parasitism, aq_{1x}	Unknown, aq_{2x}
2005	Early	Spring wheat	0.066	1	0.066	0	0.066
	Middle		0.029	0.934	0.028	0	0.028
	Late		0.023	0.907	0.907	0	0.021
	Total				1	0	0.114
2006	Early	Spring wheat	0.044	1	0.044	0	0.044
	Middle		0.141	0.956	0.135	0.010	0.125
	Late		0.034	0.821	0.821	0	0.028
	Total				1	0.010	0.196
2007	Early	Winter wheat	0.189	1	0.189	0.010	0.179
	Middle		0.299	0.811	0.242	0.006	0.236
	Late		0.139	0.569	0.569	0.003	0.076
	Total				1	0.012	0.490

aq_x Fraction of deaths from all causes in stage x given that the individual is alive at the beginning of stage x, al_x fraction of survivors at stage x out of original cohort of al_1, ad_x fraction of deaths in stage x from all causes, aq_{ix} fraction of deaths from cause i in stage x in the presence of all other causes given that the individual is alive at the beginning of stage x

year of the study, including all Conrad data (US-NOAA 2011). The recorded minimum temperature in Amsterdam in 2007 was 3°C greater than the next hottest site-year of the study, including Conrad. The recorded difference is much greater than the nearly identical 30 year average between the two sites (Fig. 1). It is likely that the high temperatures resulted in an increase in mortality in 2007 because temperatures ≥35°C can result in adverse effects (Holmes 1979) or mortality (Pallipparambil 2006) in metamorphosing WSS larvae in the stubble of these hollow stem wheat cultivars.

Table 3 Total percentage mortality and irreplaceable mortality by location and year for wheat stem sawfly pre-diapause larvae, *Cephus cinctus* Norton. Numbers in parentheses are the percentages of mortality in the presence of the other factor

Location and year	Percent total mortality	Percent irreplaceable mortality	
		Parasitism	Unknown
Conrad 2005	68	35 (43)	16 (25)
Conrad 2007	68	23 (30)	26 (38)
Conrad 2008	74	22 (27)	28 (46)
Amsterdam 2005	11	0 (0)	11 (11)
Amsterdam 2006	21	1 (1)	20 (20)
Amsterdam 2007	51	1 (2)	49 (49)

The replaceable mortality (100% irreplaceable mortality) of the unknown factors by parasitism at the Conrad location was greater than the replaceable mortality of parasitism by the unknown factors (Table 3). Even though different cultivars were planted across years and sites, similar trends were observed across years within a site. Therefore, we believe this suggests that the differences observed for mortality from parasitism in this study were consistent and not primarily affected by cultivar, especially given that all were hollow stemmed.

Discussion

In many temperate cropping systems, parasitism has a low irreplaceable mortality, which may explain considerable variability in efficacy with biological control, especially with exophagous feeders. However, because WSS is endophagous and protected within the stem during the entire larval developmental period in the summer, parasitism seems to be an important contributor to reducing numbers of larvae for this pest species. From a practical perspective, then, manipulation of parasitism through augmentative releases or parasitoid conservation for WSS specifically, and other endophagous pests more generally, may be beneficial because of the high levels of irreplaceable mortality from this factor.

Previous studies have also shown that the presence of braconid parasitoids can lead to a decrease in WSS populations in Canada and Montana (Ainslie 1929; Holmes et al. 1963; Morrill 1998; Morrill et al. 1994;

Nelson and Farstad 1953). However, the occurrence and abundance of these parasitoids, and therefore their effectiveness in acceptable management of the WSS, has been highly variable. The main factors affecting this variability include the host species or cultivar, seeding date, WSS infestation, and weather (Holmes et al. 1963). Moreover, parasitoid populations are difficult to maintain in an agricultural setting because they overwinter in the wheat stems, which are more commonly removed from the field at harvest under conditions where the crop density and biomass are greater, due to future interference with planting in no-till systems. As characterized above, this scenario fits the Amsterdam location better than Conrad with higher yielding crops due to greater amounts of precipitation (Fig. 1) and also to a higher proportion of irrigated acres where the straw must be removed because of the unwieldy postharvest crop biomass. Thus, conservation of braconid parasitoids through the use of agronomic practices that pose the least disturbance to parasitoid habitat is encouraged, although this may pose a challenge when crops are particularly robust. These practices include no-till or limited tillage for weed management and increasing stubble height during harvest because they lead to less disturbance of the standing wheat stems where parasitoids overwinter after harvest. To conserve parasitoids, it is recommended to leave at least one-third of the length of the standing crop undisturbed during harvest (Meers 2005) and to limit tilling to manage weeds (Runyon et al. 2002).

Augmentative increases of parasitoids may prove beneficial in locations where natural populations do not occur in significant numbers. Efforts to rear these parasitoids in large numbers in indoor insectaries have not been successful but mass rearing has been shown to be possible in outdoor walk-in cages (Pallipparambil 2006). Also, relocation of parasitoids may be achieved by collecting and redistributing infested stubble from fields containing high densities of parasitoids.

In this study, we used well-established demographic analytic methods to reveal the mortality dynamics of parasitism for WSS. The organizational and analytic construct of the multiple decrement life table has allowed us to identify aspects of the mortality dynamics and role of parasitism of pre-diapause summer WSS larvae that are not available using conventional life table approaches or simple

statistics of percentage parasitism. In this particular system, the data suggest that parasitism—and the manipulation of parasitism—has the potential to be effective in reducing populations of the injurious stage of WSS.

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