Assessing phenological synchrony between the Chinese sawfly, *Cephus fumipennis* (Hymenoptera: Cephidae), its egg-larval parasitoid, *Collyria catoptron* (Hymenoptera: Ichneumonidae), and the North American sawfly, *Cephus cinctus*: implications for biological control

Tatyana A. Rand,[4] Wendell L. Morrill, Justin B. Runyon,[1] Kim A. Hoelmer,[2] Thomas G. Shanower,[3] Jeffrey L. Littlefield, David K. Weaver

Abstract—Many pest and beneficial insects overwinter as larvae in a state of diapause, with development resuming in the spring. In these cases, rates of post-diapause development of parasitoids must be synchronised with the vulnerable life stages of their hosts. Phenological asynchrony between introduced parasitoids and their targeted hosts has limited the success of some biological control efforts. Here, we assess the potential synchrony between *Collyria catoptron* Wahl (Hymenoptera: Ichneumonidae), a parasitoid of the Chinese wheat stem sawfly, *Cephus fumipennis* Eversmann (Hymenoptera: Cephidae), which is being considered as a biological control against a novel host species, *Cephus cinctus* Norton, in North America. We compared development timing and emergence patterns of both native and exotic species of sawflies with that of the parasitoid. We found that the mean number of days between termination of larval diapause and adult eclosion varied by less than one day across species, and patterns of emergence were also similar. The rate of development of this egg-larval parasitoid was within the range necessary to attack *C. cinctus* eggs. Furthermore, the development of *C. cinctus* from western Montana, United States of America most closely matched that of the parasitoid, suggesting western Montana as a possible release area.

Introduction

Synchrony in the seasonal phenology of parasitoids and their hosts can be a critical factor impacting parasitoid population dynamics (Godfray *et al.* 1994) with important implications for the success of classical biological control programmes (Stiling 1993; Barlow *et al.*1994; Quicke 2015). Although additional factors certainly contribute to the success or failure of introduced natural enemies

Received 21 May 2015. Accepted 21 July 2015. First published online 7 December 2015.

T.A. Rand,[4] Northern Plains Agricultural Research Laboratory, United States Department of Agriculture-Agricultural Research Service, Sidney, Montana 59270, United States of America
W.L. Morrill, J.L. Littlefield, D.K. Weaver, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717, United States of America
J.B. Runyon,[1] Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717, United States of America
K.A. Hoelmer,[2] United States Department of Agriculture-Agricultural Research Service, European Biological Control Laboratory, Montferrier-sur-Lez, France
T.G. Shanower,[3] Northern Plains Agricultural Research Laboratory, United States Department of Agriculture-Agricultural Research Service, Sidney, Montana 59270, United States of America

[1]Present address: Rocky Mountain Research Station, United States Department of Agriculture-Forest Service, 1648 S. 7th Avenue, Bozeman, Montana 59717, United States of America.

[2]Present address: United States Department of Agriculture-Agricultural Research Service, Beneficial Insects Introduction Research, 501 S. Chapel St., Newark, Delaware 19713-3814, United States of America.

[3]Present address: United States Department of Agriculture-Agricultural Research Service, Pacific West Area Office, Albany, California 94710, United States of America.

[4]Corresponding author (e-mail: tatyana.rand@ars.usda.gov).
Subject editor: Keith Summervitle
doi:10.4039/tce.2015.64

(Stiling 1993), synchronisation of life cycles of the pest and natural enemy is particularly important for specialist parasitoids attacking a univoltine host: to be successful the parasitoid must be foraging when the relevant stage of the host is present (Coppel and Mertins 1977; Quicke 2015). Therefore, to predict the potential for successful establishment in North America of a sawfly-specific egg-larval parasitoid from China, *Collyria catoptron* Wahl (Hymenoptera: Ichneumonidae), the annual development of the parasitoid's host in China, *Cephus fumipennis* Eversmann (Hymenoptera: Cephidae), and the target sawfly pest in North America, *Cephus cinctus* Norton (Hymenoptera: Cephidae), was compared with that of the parasitoid. This study was conducted as an early step in evaluating the biocontrol potential of this egg-larval parasitoid given that developmental synchrony is a critical factor determining the potential establishment and success of this natural enemy.

The first specimens of *C. cinctus* were reared from native grasses in North America (Norton 1872; Ainslie 1929). Infestations were first observed in spring wheat in Manitoba, Canada in 1895, Saskatchewan, Canada in 1907, and losses were heavy in Montana, North Dakota, and South Dakota (United States of America) by 1920 (Fletcher 1896; Wallace and McNeal 1966). Damage also appeared in Montana winter wheat by 1980 (Morrill and Kushnak 1996), and losses continue to be extensive across its historical range in Montana, North Dakota, and some areas of the adjacent Canadian provinces (Nansen *et al*. 2005; Beres *et al*. 2011). Furthermore, the economic range of the pest is expanding south with economic infestations now reported from Wyoming, Colorado, and Nebraska (United States of America) (Peairs *et al*. 2010). *Cephus cinctus* has historically been considered native to North America, but its possible discovery in northeastern Asia (Ivie and Zinovjev 1996) has led to some uncertainty regarding its origin. The related *Cephus fumipennis* also causes significant losses of wheat in its native China (Zhao 2000; Chen *et al*. 2004). The lack of adequate control that is typically afforded by current sawfly management strategies in North America, coupled with the relatively successful biocontrol of *Cephus pygmaeus* (Linnaeus) in eastern North America (see below), has renewed interest in evaluating foreign natural enemies for biological control of these graminivorous sawflies (Shanower and Hoelmer 2004; Hoelmer and Shanower 2004).

The natural histories of *C. cinctus* and *C. fumipennis* are similar (Shanower and Hoelmer 2004). During the winter, sawfly larvae are located within the lower regions of cut stems. The larvae are in a state of obligatory diapause, which is completed after about three months of low temperatures (Salt 1947). Larval development resumes in the spring after ambient and soil temperatures increase. There is a brief pupal stage, followed by adult emergence. At emergence, the oviduct contains mature eggs (Ainslie 1929), there is no pre-oviposition period and females begin host location and oviposition soon after eclosion, irrespective of mating status (Weiss *et al*. 1987; Morrill *et al*. 2001). The females insert eggs into the lumen of the stems of host plants. The larvae feed along the length of the stem interior and complete their development within the stems. Circular notches are cut around the interior perimeter of stems, which usually lodge or break before harvest. Feeding by larvae reduces the amount of grain that is produced, and additional losses also occur because lodged stems cannot easily be retrieved at harvest (Beres *et al*. 2011). There is one generation per year.

Cephus cinctus populations in feral grasses are hosts for several species of presumably native parasitoids (Ainslie 1929). Two braconid species, *Bracon cephi* (Gahan) (Davis *et al*. 1955; Holmes *et al*. 1963; Morrill *et al*. 1994; Morrill and Gabor 1998) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae) (Runyon *et al*. 2001, 2002; Weaver *et al*. 2004, 2005; Cárcamo *et al*. 2012), currently attack *C. cinctus* larvae in wheat fields. These parasitoids are bivoltine; first generation larvae of both species develop rapidly, adults emerge and go on to a partial or complete second generation (Nelson and Farstad 1953; Somsen and Luginbill 1956). Adult parasitoids insert eggs through stem walls and onto the host larvae, which are paralysed at the time of attack (Nelson and Farstad 1953). Host larvae are consumed before the second-generation parasitoid larvae overwinter in cocoons within stems or stubs, and the adult parasitoids emerge during the following late spring or early summer. There are no known egg-larval parasitoids of *C. cinctus* populations in wheat fields in North America.

In China, *C. fumipennis* is attacked by the egg-larval parasitoid, *Collyria catoptron* Wahl (Hymenoptera: Ichneumonidae) (Wahl *et al*. 2007). The natural history is likely similar to that of *Collyria*

coxator (Villers), which attacks the closely related *Cephus pygmaeus* (Salt 1931; Filipy *et al*. 1985; Shanower and Hoelmer 2004), which is an introduced species in North America. Adult parasitoids oviposit within newly deposited sawfly eggs, the parasitoid eggs develop and hatch before host eggs, and larvae develop within the sawfly larvae, which continue to feed. Parasitised sawfly larvae complete development, move to the base of the plants and cut the stems. The following spring the parasitoid larvae break diapause, pupate, and the adults emerge (Salt 1931). Since parasitoids do not kill larvae until after cutting damage has occurred, any benefits from the biological control perspective would have a time lag, being realised through reduced wheat stem sawfly populations the following year.

An extensive programme to introduce European parasitoids into eastern North America for control of the introduced *C. pygmaeus* was undertaken several decades ago (Shanower and Hoelmer 2004). As a result, *C. coxator* was established in eastern Canada after releases in 1940 (Smith 1959; Turnbull and Chant 1961) and later in the eastern United States of America (Streams and Coles 1965), and appears to play a role in regulating *C. pygmaeus* populations (Filipy *et al*. 1985; Shanower and Hoelmer 2004). Releases of this parasitoid for control of *C. cinctus* in the northern Great Plains from 1930 to 1939 were not successful. This failure has been attributed to lack of seasonal synchronisation, poor climate matching, and/or high population densities of the cannibalistic sawfly larvae (Smith 1959; Turnbull and Chant 1961; Beirne 1975). To better match the natural enemy with the target environment, *Collyria catoptron* was collected from semi-arid northern China, which has a continental climate similar to that of Montana. Our study was designed to compare the number of days between the termination of obligatory larval diapause and adult emergence of the two sawfly species and their associated parasitoids and assess overlap in emergence duration among species. Similar post-diapause development times and emergence patterns for *C. fumipennis*, *C. cinctus*, and *Collyria catoptron* would indicate similar phenologies, such that the lack of suitable hosts would not be predicted to be a limiting factor for foraging *C. catoptron*. Post-diapause synchrony of the two sawfly species would also indicate that suitable *C. fumipennis* larvae should be available for foraging females of *B. cephi* and *B. lissogaster* if these were to be considered for introduction in Asia.

Materials and methods

Sources of insects

Post-harvest wheat stubs containing sawfly larvae and associated parasitoids were collected in the fall of 2002 from northern China and Montana, United States of America. Eleven collection sites were selected in Gansu Province in China. These included: Yuzhong County (Shanjiao, Gancao, Xiaokangying, and Chengguan townships), Gaolan County (Shuifu and Shidong townships), and Yongdeng County (Liancheng and Hequiao townships). Although global positioning system coordinates for each field used in this study were not recorded, coordinates for nearby fields in each county recorded in 2005 were as follows: Yuzhong (35.889167°N, 104.151389°E); Gaolan (36.315833°N, 103.936111°E); Yongdeng (36.743611°N, 103.2425°E). All sites were located within 100 km from Lanzhou (36°N latitude). Collections were made from 21 to 25 August and again from 12 to 19 October.

Sawfly-infested wheat stubs were also collected from five fields within several counties in Montana in 2002. Three western sites were selected and material was collected on 24–25 October in Broadwater (46.0120°N, 111.5842°W) and Gallatin Counties (45.8161°N, 111.5967°W and 45.8010°N, 111.5167°W), which were approximately 550 km from the two eastern sites in Valley (48.8375°N, 106.3250°W) and Daniels Counties (48.7458°N, 105.1658°W). Sawfly-infested material was collected on 6–7 November from Valley County and on 25 September and 3 November from Daniels County.

Handling of insects

Sawfly-containing stubs of both species were shipped to quarantine facilities at Montana State University (MSU) in Bozeman, Montana, United States of America, as well as the United States Department of Agriculture-Agricultural Research Service, European Biological Control Laboratory (EBCL) in Montferrier-sur-Lez, France. Stubs were placed in plastic bags and held at 4 °C and 35% relative humidity for about five months to permit completion of larval diapause. The bags were occasionally opened and stubs were lightly misted with water to prevent desiccation. The exact duration of the diapause requirement was unknown, so cohorts of larvae were removed from cold incubation conditions in a weekly sequence to increase the

potential for successful metamorphosis. Specifically, groups of 30 stubs were removed from cold storage at four weekly intervals (19 May, 26 May, 2 June, and 9 June at MSU; and 20 May, 30 May, 3 June, and 10 June at EBCL). Stubs were then placed in 400 mL clear plastic containers which were held at 25 ± 2 °C, 35% relative humidity, with a 14 light:10 dark hours photoperiod. The emergence of adult sawflies and parasitoids was recorded daily.

Statistical analysis

The post-diapause periods (PDP), or number of days between termination of cold storage and adult emergence, were compared for the two species of sawflies and the parasitoid species. Data were analysed using a mixed model approach (Proc Mixed, SAS version 8.2, Cary, North Carolina, United States of America) with laboratory, sex, and species treated as fixed effects; removal date was treated as a random effect. Treating removal date as a random effect incorporated this variation into the analysis and although we did not explicitly test for differences, there was no trend for either lengthening or shortening the developmental period as the removal date changed. We treated the site variable (nested within country) as random when examining overall differences in the PDP (where sites are treated as random samples from a larger population and we wanted to make an assessment regarding the larger population) or fixed to determine if the PDP differed between sites and if so, where parasitoids should be collected and released to maximise the probability of successful establishment. All data were natural log transformed to meet the assumptions of normality.

Estimating host-parasitoid phenological overlap

We compared overlap in emergence patterns and duration between the hosts, *C. cinctus*, from eastern and western Montana populations, as well as the Chinese host, *C. fumipennis* (populations from different counties in this case were lumped since no significant differences were found in PDP, see Table 2), and the parasitoid, *C. catoptron*. To do so we plotted the proportion of female individuals emerging through time for each species (Fig. 1), and fit curves to these data using the nonlinear modelling platform in JMP version 10 (SAS Institute Inc. 2010). Additionally, we constructed a figure to visualise the potential availability of the susceptible stage of both host sawfly species to ovipositing *C. catoptron* females (Fig. 2). Data on adult female emergence timing, adult longevity, and the average egg development time were combined to show the expected duration of life stages. As stated earlier, the natural histories of the two cephid species are similar (Shanower and Hoelmer 2004). For example, the reported 7.5 days for adult female longevity of *C. cinctus* (Morrill *et al.* 2000) is very similar to the seven to eight days for adult longevity of *C. fumipennis* reported from several studies in China by Chen *et al.* (2004). Longevity data were added to the mean number of days required for emergence of adult cephid females from each population, assessed in the present study, and displaced by a further seven-day pre-hatch interval (Ainslie 1929) for the eggs from the last surviving female (Fig. 2).

Results

Effects of laboratory, collection date, and sex on development

The PDP of more than 1000 individual insects was recorded (Table 1). Overall there was no difference in the PDP between the MSU and EBCL laboratories ($F = 1.81$, $P = 0.179$) nor did collection date influence the PDP of any species ($P > 0.05$). Because previous studies showed that males of *C. cinctus* emerged earlier than females (Cárcamo *et al.* 2005), we tested whether there was a difference in the PDP between sexes. The mean PDP for males of *C. catoptron* is reported, but these data were removed for this analysis since only five males of this species emerged during the study. *Collyria catoptron* populations sampled thus far are heavily female biased, with males produced only rarely (Wahl *et al.* 2007). Sawfly males emerged approximately one day earlier than females (sex, $F = 45.72$, $P < 0.001$) and this was true for both sawfly species (species × sex, $F = 0.03$, $P = 0.869$) (Table 1). Data for males and females were separated for further analysis.

Overall comparison of sawfly and parasitoid development

There was no difference in the PDP between males of *C. cinctus* and males of *C. fumipennis* (Table 1). The mean PDP for females of *C. cinctus, C. fumipennis,* and the parasitoid *C. catoptron* was significantly different, but varied by less than one day (Table 1).

Table 1. Post-diapause development (days ± SEM) of the North American wheat stem sawfly *Cephus cinctus*, the Chinese wheat stem sawfly *Cephus fumipennis*, and its parasitoid *Collyria catoptron*.

Species	Male (*n*)	Female (*n*)	Total (*n*)
Cephus cinctus	25.2 ± 0.3 (167)	26.2 ± 0.2 (252)	419
Cephus fumipennis	24.7 ± 0.3 (199)	26.0 ± 0.2 (286)	485
Collyria catoptron	25.8 ± 2.9 (5)	25.9 ± 0.3 (176)	181
Column comparison	$F = 0.06$	$F = 4.35$	
	$P = 0.810$*	$P = 0.035$	

Note: * Data for males of *Collyria* not included in comparison due to small sample size ($n = 5$).

Table 2. Comparison of post-diapause development (days ± SEM) of the North American sawfly *Cephus cinctus* from different locations in Montana, United States of America and the Chinese sawfly *Cephus fumipennis* and its parasitoid *Collyria catoptron* from locations in Gansu Province, China.

		PDP (days ± SEM)				
		Cephus cinctus		*Cephus fumipennis*		*Collyria catoptron*
Country	Collection site (county)	Male (*n*)	Female (*n*)	Male (*n*)	Female (*n*)	Female (*n*)
United States of America	Broadwater; Gallatin (western Montana)	23.7 ± 0.3 (115)	25.3 ± 0.2 (211)	–	–	–
United States of America	Valley; Daniels (eastern Montana)	28.5 ± 0.5 (52)	30.4 ± 0.5 (41)	–	–	–
China	Yuzhong	–	–	24.9 ± 0.4 (133)	25.8 ± 0.3 (165)	26.1 ± 0.3 (134)
China	Gaolan	–	–	24.7 ± 0.9 (24)	25.8 ± 0.3 (165)	27.1 ± 0.6 (8)
China	Yongdeng	–	–	24.1 ± 0.6 (42)	27.2 ± 0.5 (56)	25.2 ± 0.5 (34)
Column comparison		$F = 93.77$	$F = 94.18$	$F = 2.11$	$F = 1.31$	$F = 0.37$
		$P < 0.001$	$P < 0.001$	$P = 0.125$	$P = 0.271$	$P = 0.690$

Note: PDP, post-diapause period.

Comparison of sawfly and parasitoid development among counties

Having established that overall there was little or no difference in the PDP between the two sawfly species and the parasitoid, we next wanted to see if there were developmental differences between locations (*i.e.*, county) within each country. If so, collection and release sites could be chosen to optimise phenological synchrony of host and parasitoid and thus improve the chances of successful establishment. There were no differences in the PDP for either males or females of *C. fumipennis* or its parasitoid *C. catoptron* among the sampled counties in China, that were relatively close to one another (⩽150 km) (Table 2). However, across the larger spatial gradient in Montana (550 km) both males and females of *C. cinctus* emerged about five days earlier when collected from populations from western Montana compared with those from eastern Montana (Table 2). We next compared the PDP of *C. cinctus* from eastern and western Montana with the PDP of *C. fumipennis* and *C. catoptron* from China. The PDP of male ($F = 10.14$, $P = 0.002$) and female ($F = 10.62$, $P = 0.001$) *C. cinctus* from eastern Montana was longer than *C. fumipennis* and *C. catoptron* from China. However, there was no difference in the PDP between *C. fumipennis* and *C. catoptron* and males ($F = 1.62$, $P = 0.205$) or females ($F = 3.08$, $P = 0.080$) of *C. cinctus* from western Montana.

Estimating host-parasitoid phenological overlap

The best-fit curves (lowest corrected Aikake Information Criterian values) to the emergence data for all insect species/populations were Gaussian peak

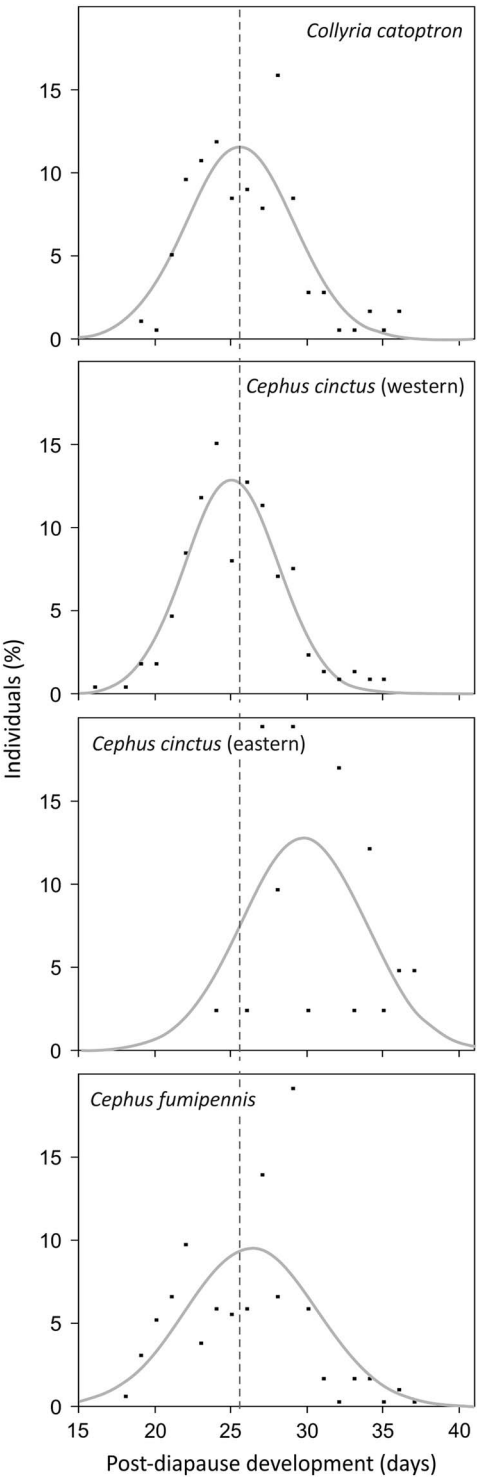


Fig. 1. The percentage of female individuals emerging through time (days post-diapause) for the parasitoid, *Collyria catoptron*, and the potential host species the North American sawfly (*Cephus cinctus*), both western and eastern populations and the Chinese sawfly (*Cephus fumipennis*). Best-fit Gaussian peak curves are presented, with the dotted line representing peak emergence for *C. catoptron*, to aid in comparisons with other species.

curves (Fig. 1) although explanatory power varied across groups ($R^2 = 0.24$ for *C. cinctus* eastern populations; $R^2 = 0.88$ for *C. cinctus* western populations; $R^2 = 0.73$ for *C. catoptron*; $R^2 = 0.44$ for *C. fumipennis*). Minimum-maximum PDP varied only slightly for three of four insect groups: *C. cinctus* from western Montana (16–35 days), *C. fumipennis* (18–37 days), and *C. catoptron* (19–36); furthermore >89% of the individuals emerged in a relatively tight window between 20 and 30 days post diapause for these three groups (Fig. 1). In contrast, *C. cinctus* from eastern Montana began emerging later (24 days) and continued emerging longer (37 days). The vulnerable egg stages of both host species, *C. fumipennis* and *C. cinctus* (both western and eastern populations), are projected to overlap with adult female *C. catoptron* flight (Fig. 2).

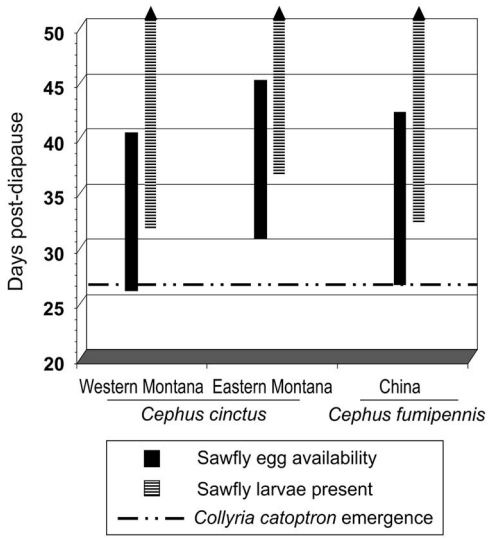
Development of the *Cephus cinctus* larval parasitoid *Bracon cephi*

We recorded the PDP of *B. cephi* that emerged from the eastern Montana sites. No *C. cinctus* parasitoids were obtained from stubs collected from the western Montana populations, although parasitoids could have been present within the stems, which were not sampled. Previous work has shown that parasitism in these western Montana locations can be substantial (Runyon *et al*. 2002). The average PDP for *B. cephi* was 26.4 ± 0.9 days ($n = 86$). Males of *B. cephi* emerged approximately six days earlier than females (23.1 ± 1.2 and 29.0 ± 1.0 days for males and females, respectively) ($F = 35.17$, $P < 0.001$).

Discussion

Synchrony in the seasonal phenology of parasitoids and their host insects is an important factor impacting parasitoid population dynamics (Godfray *et al*. 1994) and plays an often crucial role in determining the success of classical biological control programmes (Stiling 1993). For example, mismatches in the seasonal development of sawflies and parasitoids has been suggested as one of the factors responsible for the failure of the early

Fig. 2. Predicted number of days *Cephus cinctus* and *C. fumipennis* larvae and eggs would be present after completion of larval diapause. Predictions are based on the mean emergence of females, female longevity, and egg development time. The dashed horizontal line shows the mean emergence time of females of the parasitoid, *Collyria catoptron*.



attempt to establish European egg-larval parasitoids in the northern Great Plains of the United States of America and Canada (Smith 1959; Turnbull and Chant 1961; Beirne 1975). As such, knowledge of the seasonal activity of adult *C. cinctus* and *C. fumipennis* was needed as an initial step to evaluate the potential suitability of *C. cinctus* as a host for the egg-larval parasitoid *C. catoptron*. Because these insects overwinter as larvae in a state of diapause in wheat stubble, with development resuming in the spring, similar rates of post-diapause development (PDP) are critical to ensuring that parasitoids encounter the vulnerable life stages of their hosts upon emergence.

Across all studied populations, we found that mean PDP of all three insects was very similar, varying less than a day (Table 1). Overlap in emergence timing was also substantial for three groups of insects, *C. cinctus* from western populations, *C. fumipennis* and *C. catoptron,* with $\geqslant 89\%$ of individuals emerging between 20 and 30 days post-diapause, and peak emergence between 25 and 26 days post-diapause (Fig. 1). Eastern Montana *C. cinctus* populations were less well synchronised with *C. catoptron*, with both first and peak emergence about five days later than the parasitoid. Projection of the duration of life-history stages indicated that the vulnerable host stage (eggs) of *C. cinctus* would be available to *C. catoptron* upon emergence for western Montana populations, and less than a week from mean emergence time for the eastern Montana populations (Fig. 2). Thus overall, our data indicate that the Chinese and North American sawfly species are very similar in their seasonal development, and that *C. cinctus* eggs should be present for foraging *C. catoptron* if it were to be released in North America.

The population differences in egg availability highlighted in Figure 2 reflect significant differences in PDP among Montana sawfly populations. Both mean and peak emergence of western populations occurred earlier than eastern populations (Fig. 1; Table 2); no such differences were observed among Chinese populations (Table 2). The lack of differences in emergence timing among sawflies from the Chinese populations is not surprising, given their relative proximity ($\leqslant 150$ km) and lack of geographic barriers among them. In contrast, populations in eastern and western Montana were much more isolated from one another (~550 km) and span a major gradient in precipitation (Rand *et al.* 2014). These findings support previous observations that sawflies from western Montana emerge earlier than those from eastern Montana (Lou *et al.* 1998; Perez-Mendoza and Weaver 2006). Although western Montana collection locations in the current study were also farther south than those in eastern Montana, previous work shows similar differences in emergence timing between western populations collected farther north (Pondera County; 48.17°N, 111.95°W) and those in northeastern Montana (Valley County: 48.5°N, 106.19°W) (Lou *et al.* 1998; Perez-Mendoza and Weaver 2006), suggesting that the observed differences are associated with longitude rather than latitude. Genetic studies further show that there are differences in mitochondrial DNA sequences among sawfly populations from various locations across the northern Great Plains of the United States of America and Canada (Bon *et al.* 2005), which corroborates the findings in Lou *et al.* (1998). Similar differences might be expected between northern versus southern populations of *Cephus* in China or the United States of America, however this remains

to be determined. Since minor genetic differences among insect populations can impact the suitability as hosts for biocontrol agents (Wajnberg 2004; Hufbauer and Roderick 2005), these differences may be important and warrant further investigation.

The fact that sawfly adults are now appearing nearly a month earlier than previously observed in western Montana (Morrill and Kushnak 1996), should provide a greater probability for overlap between host oviposition and foraging populations of *C. catoptron*. Specifically, our findings suggests that *C. catoptron* collected from the Chinese locations used in this study are better synchronised with *C. cinctus* populations from western Montana, increasing the potential for successful establishment there. However, population differences might not limit the potential success of *C. catoptron* in eastern Montana because adult emergence periods in field situations are often variable (Ainslie 1929; Wallace and McNeal 1966). Morrill and Kushnak (1996) report the duration of adult *C. cinctus* flight in western Montana ranging from 9 to 34 days, with slightly less variable duration observed over eight site-years in North Dakota (14–27 days; Stegmiller 2012). Thus, establishment failure due to reduced egg availability in the field for eastern populations would be unlikely. A more important consequence of the lack in synchrony might be the potential for late emerging *C. cinctus* to escape parasitism by *C. catoptron*. However, relatively rapid shifts in diapause timing by biocontrol agents to be better synchronised with the phenology of their host populations have been observed in other systems (Bean *et al*. 2012), which could improve synchrony and effectiveness over time.

Bracon cephi is a larval parasitoid that successfully parasitises *C. cinctus* in Montana wheat fields (Weaver *et al*. 2004, 2005). Furthermore, parasitism can be extensive in some fields, with maximum observed parasitism rates exceeding $\geqslant$ 88% (Morrill *et al*. 1994; Rand *et al*. 2014), and can also attenuate physiological loss (Macedo *et al*. 2007; Delaney *et al*. 2010) in wheat head weight for infested stems (Buteler *et al*. 2008). The seasonal activity of *B. cephi* generally parallels that of its host *C. cinctus*, although it has a longer flight period (Stegmiller 2012; Davis 2013). The similarity in development between *C. cinctus* and *C. fumipennis* thus suggests that *B. cephi* would likely encounter suitable stages of *C. fumipennis* in China. The adult females of this parasitoid species have a pre-oviposition period of three weeks in the first generation, during which the eggs mature, which would ensure that the required larger sawfly larvae are available to ovipositing parasitoids (Nelson and Farstad 1953). No additional parasitoid species of either wheat stem sawfly species were found, although a few specimens of the predator, *Phyllobanius dubius* (Wolcott) (Coleoptera: Cleridae) (Morrill *et al*. 2001), were recovered from *C. cinctus* stubs.

In summary, the findings presented here suggest that lack of developmental synchrony will not be a factor that limits successful establishment of *C. catoptron* for control of *C. cinctus* in North America. However, while neither a lack of climatic matching nor host-parasitoid phenological asynchrony are predicted to be impediments to the potential success for this agent, preliminary results from additional studies suggest a basic physiological incompatibility between *C. cinctus* and *C. catoptron*. Rand *et al*. (2015) found that while *Collyria catoptron* oviposits and initiates larval development within *C. cinctus*, it never completed development and emerged as an adult from the novel host.

Acknowledgements

The authors thank Hongyin Chen (United States Department of Agriculture-Agricultural Research Service; Sino-American Biological Control Laboratory, Beijing) and Aiping Liu (Chinese Academy of Agricultural Sciences, Grasslands Research Institute, Hohhot, Inner Mongolia) for their assistance in obtaining the samples from China, and J. Zhu (Penn State) for help with the statistical analysis. Norma Irish provided valuable technical assistance. Research conducted at Montana State University was supported by the Montana Wheat and Barley Committee and the Montana Agricultural Experiment Station.

References

Ainslie, C.N. 1929. The western grass-stem sawfly, a pest of small grains. Bulletin 157. United States Department of Agriculture, Washington, District of Columbia, United States of America.

Barlow, N.D., Goldson, S.L., and McNeill, M.R. 1994. A prospective model for the phenology of *Microctonus hyperodae* (Hymenoptera: Braconidae), a potential biological control agent of argentine stem weevil in New Zealand. Biocontrol Science and Technology, **4**: 375–386.

Bean, D.W., Dalin, P., and Dudley, T.L. 2012. Evolution of critical day length for diapause induction enables range expansion of *Diorhabda carinulata*, a biological control agent against tamarisk (*Tamarix* spp.). Evolutionary Applications, **5**: 511–523. doi:10.1111/j.1752-4571.2012.00262.x.

Beirne, B.P. 1975. Biological control attempts by introductions against pest insects in the field in Canada. The Canadian Entomologist, **107**: 225–236.

Beres, B.L., Cárcamo, H.A., Weaver, D.K, Dosdall, L.M., Evenden, M.L., Hill, B.D., *et al*. 2011. Integrating the building blocks of agronomy and biocontrol into an IPM strategy for wheat stem sawfly. Prairie Soils and Crops Journal, **4**: 54–64.

Bon, M.C., Shanower, T., Morrill, W., Hoelmer, K., Hurard, C., and Martin, J.F. 2005. Improving biological control of an invasive pest with molecular phylogeographic and population genetic approaches: the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) as a case study. Proceedings of the 7th International Conference on Pests in Agriculture, Montpellier, France, 26–27 October 2005. Published on CD-ROM, Montpellier, France.

Buteler, M., Weaver, D.K., and Miller, P.R. 2008. Wheat stem sawfly infested plants benefit from parasitism of the herbivorous larvae. Agricultural and Forest Entomology, **10**: 347–354. Corrigendum **11**: 123.

Cárcamo, H.A., Beres, B.L., Clarke, F., Byers, R.J., Mundell, H.H., May, K., *et al*. 2005. Influence of plant host quality on fitness and sex ratio of the wheat stem sawfly (Hymenoptera: Cephidae). Environmental Entomology, **34**: 1579–1592.

Cárcamo, H.A., Weaver, D.K., Meers, S.B., Beres, B.L., and Mauduit, A.L. 2012. First record of *Bracon lissogaster* (Hymenoptera: Braconidae) in Canada – a potentially important parasitoid of *Cephus cinctus* (Hymenoptera: Cephidae) in the prairies. Biocontrol Science and Technology, **22**: 367–369.

Chen, S., Hoelmer, K.A., Chen, H., Liu, A., and Shanower, T.G. 2004. A review of wheat stem sawfly (Hymenoptera: Cephidae) research in China. Journal of Agricultural and Urban Entomology, **21**: 249–256.

Coppel, H.C. and Mertins, J.W. 1977. Biological insect pest suppression. Springer-Verlag, New York, New York, United States of America.

Davis, E.G., Benton, C., and Somsen, H.W. 1955. Natural enemies of the wheat stem sawfly in North Dakota and Montana. North Dakota Bimonthly Bulletin, **28**: 63–65.

Davis, R.A. 2013. Mechanisms for reproductive isolation in two congeneric parasitoids of the wheat stem sawfly. M.S. thesis. Montana State University, Bozeman, Montana, United States of America. Available from http://scholarworks.montana.edu/xmlui/handle/1/3477 [accessed 25 September 2015].

Delaney, K.J., Weaver, D.K., and Peterson, R.K.D. 2010. Wheat photosynthesis and yield reductions: wheat stem sawfly (Hymenoptera: Cephidae) herbivory interacts with abiotic conditions and host plant resistance. Journal of Economic Entomology, **103**: 516–524.

Filipy, F.L., Burbutis, P.P., and Fuester, R.W. 1985. Biological control of the European wheat stem sawfly in Delaware (Hymenoptera: Cephidae). Environmental Entomology, **14**: 665–668.

Fletcher, J. 1896. The western wheat stem sawfly (*Cephus pygmaeus* L.). Dominion of Canada, Department of Agriculture, Report of the Dominion Entomologist, **1896**: 147–149.

Godfray, H., Hassell, M., and Holt, R. 1994. The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. Journal of Animal Ecology, **63**: 1–10.

Hoelmer, K.A. and Shanower, T.G. 2004. Foreign exploration for natural enemies of cephid sawflies. Journal of Agricultural and Urban Entomology, **21**: 223–238.

Holmes, N.D., Nelson, W.A., Peterson, L.K., and Farstad, C.W. 1963. Causes of variations in effectiveness of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae) as a parasite of the wheat stem sawfly. The Canadian Entomologist, **95**: 113–126.

Hufbauer, R.A. and Roderick, G.K. 2005. Microevolution in biological control: mechanisms, patterns, and processes. Biological Control, **35**: 227–239.

Ivie, M.A. and Zinovjev, A.G. 1996. Discovery of the wheat stem sawfly (*Cephus cinctus* Norton) (Hymenoptera: Cephidae) in Asia, with the proposal of a new synonymy. The Canadian Entomologist, **128**: 347–348.

Lou, K.F., Weiss, M.J., Bruckner, P.L., Morrill, W.L., Talbert, L.E., and Martin, J.M. 1998. RAPD variation within and among geographic populations of wheat stem sawfly (*Cephus cinctus* Norton). Journal of Heredity, **4**: 329–335.

Macedo, T.B., Weaver, D.K., and Peterson, R.K.D. 2007. Photosynthesis in wheat at the grain filling stage is altered by larval wheat stem sawfly (Hymenoptera: Cephidae) injury and water limitation. Journal of Entomological Science, **42**: 228–238.

Morrill, W.L. and Gabor, J.W. 1998. Parasitism of the wheat stem sawfly (Hymenoptera: Cephidae) in Montana. Biocontrol, **12**: 159–163.

Morrill, W.L., Gabor, J.W., Weaver, D.K., Kushnak, G.D., and Irish, N.J. 2000. Effect of host plant quality on the sex ratio and fitness of female wheat stem sawflies (Hymenoptera: Cephidae). Environmental Entomology, **29**: 195–199.

Morrill, W.L. and Kushnak, G.D. 1996. Wheat stem sawfly (Hymenoptera: Cephidae) adaptation to winter wheat. Environmental Entomology, **25**: 1128–1132.

Morrill, W.L., Kushnak, G.D., Bruckner, P.L., and Gabor, G.W. 1994. Wheat stem sawfly (Hymenoptera: Cephidae) damage, rates of parasitism, and overwinter survival in resistant wheat lines. Journal of Economic Entomology, **87**: 1373–1376.

Morrill, W.L., Weaver, D.K., Irish, N.J., and Barr, W.F. 2001. *Phyllobaenus dubius* (Wolcott) (Coleoptera: Cleridae), a new record of a predator of the wheat stem sawfly (Hymenoptera: Cephidae). Journal of the Kansas Entomological Society, **74**: 181–183.

Nansen, C., Payton, M.E., Runyon, J.B., Weaver, D.K., Morrill, W.L., and Sing, S.E. 2005. Preharvest sampling plan for larvae of the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in winter wheat fields. The Canadian Entomologist, **137**: 602–614.

Nelson, W.A. and Farstad, C.W. 1953. Biology of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae), an important parasite of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae) in western Canada. The Canadian Entomologist, **85**: 103–107.

Norton, E. 1872. Notes on North American Tenthredinidae with descriptions of new species. Transactions of the American Entomological Society, **4**: 77–86.

Peairs, F.B., Hein, G.L., and Brewer, M.J. 2010. High plains integrated pest management: wheat stem sawfly. Available from http://wiki.bugwood.org/HPIPM%3AWheat_Stem_Sawfly [accessed 22 September 2015].

Perez- Mendoza, J. and Weaver, D.K. 2006. Temperature and relative humidity effects on post-diapause larval development and adult emergence in three populations of wheat stem sawfly (Hymenoptera: Cephidae). Environmental Entomology, **35**: 1222–1231.

Quicke, D.L.J. 2015. The braconid and ichneumonid parasitoid wasps: biology, systematics, evolution and ecology. Wiley Blackwell, West Sussex, United Kingdom.

Rand, T.A., Waters, D.K., Blodgett, S.L., Knodel, J.J., and Harris, M.O. 2014. Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes. Agriculture, Ecosystems and Environment, **186**: 135–143.

Rand, T.A., Waters, D.K., and Shanower, T.G. 2015. Preliminary evaluation of the parasitoid wasp, *Collyria catoptron*, as a potential biological control agent against the wheat stem sawfly, *Cephus cinctus*, in North America. Biocontrol Science and Technology. doi:10.1080/09583157.2015.1076377.

Runyon, J.B., Hurley, R.L., Morrill, W.L., and Weaver, D. K. 2001. Distinguishing adults of *Bracon cephi* and *Bracon lissogaster* (Hymenoptera: Braconidae), parasitoids of the wheat stem sawfly (Hymenoptera: Cephidae). The Canadian Entomologist, **133**: 215–217.

Runyon, J.B., Morrill, W.L., Weaver, D.K., and Miller, P. R. 2002. Parasitism of the wheat stem sawfly (Hymenoptera: Cephidae) by *Bracon cephi* and *B. lissogaster* (Hymenoptera: Braconidae) in wheat fields bordering tilled and untilled fallow in Montana. Journal of Economic Entomology, **95**: 1130–1134.

Salt, R.W. 1931. Parasites of the wheat-stem sawfly, *Cephus pygmaeus* L., in England. Bulletin of Entomological Research, **22**: 479–545.

Salt, R.W. 1947. Some effects of temperature on the production and elimination of diapause in the wheat stem sawfly, *Cephus cinctus* Nort. Canadian Journal of Research, **25**: 66–86.

SAS Institute Inc. 2010. JMP. Version 10. SAS Institute Inc., Cary, North Carolina, United States of America.

Shanower, T.G. and Hoelmer, K.A. 2004. Biological control of wheat stem sawflies: past and future. Journal of Agricultural Urban Entomology, **21**: 197–221.

Smith, R.W. 1959. Status in Ontario of *Collyria calcitrator* (Grav.) (Hymenoptera: Ichneumonidae) and of *Pediobius beneficus* (Gahan) (Hymenoptera: Eulophidae) as parasites of the European wheat stem sawfly *Cephus pygmaeus* (L.) (Hymenoptera: Cephidae). The Canadian Entomologist, **91**: 697–700.

Somsen, H.W. and Luginbill, P. 1956. *Bracon lissogaster* Mues.: a parasite of the wheat stem sawfly. United States Department of Agriculture Technical Bulletin, **1153**: 1–7.

Stegmiller, J. 2012. Pest management of wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) in western North Dakota. M.S. thesis. North Dakota State University, Fargo, North Dakota, United States of America.

Stiling, P. 1993. Why do natural enemies fail in classical biological control programs? American Entomologist **1**: 31–37.

Streams, F.A. and Coles, L.W. 1965. Wheat stem sawfly parasites, *Collyria calcitrator* and *Pediobius nigritarsis,* in eastern United States. Journal of Economic Entomology, **58**: 303–306.

Turnbull, A.L. and Chant, D.A. 1961. The practice and theory of biological control of insects in Canada. Canadian Journal of Zoology, **39**: 697–753.

Wahl, D.B., Shanower, T.G., and Hoelmer, K.A. 2007. A new species of *Collyria* Schiødte (Hymenoptera: Ichneumonidae: Collyriinae), a parasitoid of *Cephus fumipennis* (Hymenoptera: Cephidae) in China, and potential biological control agent for *Cephus cinctus* in North America. Journal of the Kansas Entomological Society, **80**: 43–50.

Wajnberg, E. 2004. Measuring genetic variation in natural enemies used for biological control: why and how? *In* Genetics, evolution, and biological control. *Edited by* L. Ehler, R. Sforza, and T. Mateille. CABI Publishing, Cambridge, Massachusetts, United States of America. Pp. 19–37.

Wallace, L.E. and McNeal, F.H. 1966. Stem sawflies of economic importance in grain crops in the United States. Agricultural Research Service, United States Department of Agriculture Technical Bulletin, **1350**: 1–50.

Weaver, D.K., Nansen, C., Runyon, J.B., Sing, S.E., and Morrill, W.L. 2005. Spatial distributions of *Cephus cinctus* Norton (Hymenoptera: Cephidae) and its braconid parasitoids in Montana wheat fields. Biological Control, **34**: 1–11.

Weaver, D.K., Sing, S.E., Runyon, J.B., and Morrill, W.L. 2004. Potential impact of cultural practices on wheat stem sawfly (Hymenoptera: Cephidae) and associated parasitoids. Journal of Agricultural and Urban Entomology, **21**: 271–287.

Weiss, M.J., Morrill, W.L., and Reitz, L.L. 1987. Influence of planting date and spring tillage on the wheat stem sawfly. Montana AgResearch, **4**: 5.

Zhao, L. 2000. Identification of the natural resistance of several spring wheat varieties to Cephus fumipennis Eversmann. Acta Agriculturae Boreali-Occidentalis Sinica, **9**: 39–40.