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ARTICLE

The impact of parasitoids on diamondback moth in Europe: a life table approach

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Abstract
Diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), was first recorded in North America from Europe about 150 years ago and can be a significant pest of canola in Western Canada. Because parasitism of *P. xylostella* in Canada is generally low, the introduction of one or more additional exotic parasitoids from Europe is being considered to increase the suppression of *P. xylostella* populations. Life table studies to determine the impact of parasitoids on diamondback moth populations in Europe were conducted in northwestern Switzerland in 2014–2016. Net reproductive rates were found to be less than one in seven out of eight life tables, suggesting that *P. xylostella* populations in Switzerland are mostly driven by immigration and recolonisation. In total, seven primary parasitoid species and one hyperparasitoid were associated with diamondback moth. Pupal parasitism by *D. collaris* reached up to 30%, but because generational mortality was mainly driven by abiotic mortality factors and predation of larvae, the overall contribution of pupal parasitism was low (< 6%). In regions of Canada, where *P. xylostella* may have increasing populations and low larval mortality, the addition of *D. collaris* may be a promising approach. Life table studies across Canada are necessary to determine the need for such intervention.

Introduction

The native range of the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), is believed to be Africa (Juric *et al.* 2017), but nowadays, the species has a global distribution and is considered the most destructive pest of Brassicaceae crops around the world, with an annual estimated cost of US$4–5 billion (Zalucki *et al.* 2012). In vegetable crops, damage is mainly caused by the larvae feeding on leaves, leaving translucent windows or 'shot holes' in the leaf blades. In canola, *Brassica napus* Linnaeus and *B. rapa* Linnaeus (Brassicaceae), damage is caused by the larvae feeding on flower buds, flowers, and developing seed pods. Extensive feeding on the reproductive plant parts can significantly reduce crop yields (Munir *et al.* 2013).

In North America, diamondback moth was first reported in the mid-nineteenth century (Fitch 1856) and now occurs throughout the continent. Populations of the moth are likely not able to overwinter north of 43° in eastern North America (Dancau *et al.* 2018); instead, there is evidence that the moths arrive from the southern United States of America and Mexico each year (Hopkinson and Soroka 2010). Populations of diamondback moth routinely infest

canola on the prairies of western Canada, where in most years, the moth causes minor economic damage. However, in 1995 and 2001, populations reached outbreak densities, resulting in spraying of pesticides on 1.25 and 1.8 million hectares of canola, respectively (Dosdall and Mason 2010). In Europe, bioclimatic models suggest that in most regions of Italy, Spain, France, and Belgium, diamondback moth can persist year-round (Zalucki and Furlong 2011).

Similar to North America, early summer infestations in central and northern Europe usually arise as a result of migrations from southern Europe, when the wind direction is favourable and when large populations of moths are ready to migrate (Chapman *et al.* 2002; Coulson *et al.* 2002; Wainwright *et al.* 2020). However, warmer winter temperatures as a result of climate change may alter the phenology and the area where the moth may persist year-round (Furlong and Zalucki 2017), as already indicated by the presence of larvae in Brassicaceae crops in mid-January 2018 in the United Kingdom (Wainwright *et al.* 2020).

Because of the development of resistance to chemical insecticides (reviewed in Furlong *et al.* 2013), which limits growing options for control and increases crop losses and production costs, the interest in sustainable control options for diamondback moth in Canada has been renewed. Although numerous parasitoid species have been reported to attack various life stages of diamondback moth (Delvare 2004; Furlong *et al.* 2013), most biological control of this species worldwide is achieved by relatively few species belonging to the hymenopteran genera *Diadegma* Förster and *Diadromus* Wesmael (Ichneumonidae), *Microplitis* Förster and *Cotesia* Cameron (Braconidae) and *Oomyzus* Rondani (Eulophidae) (reviewed in Sarfraz *et al.* 2005). Across Canada, the larval parasitoids *Diadegma insulare* (Cresson) and *Microplitis plutellae* Muesebeck and the solitary pupal endoparasitoid *Diadromus subtilicornis* (Gravenhorst) (Hymenoptera: Ichneumonidae) are the dominant species attacking diamondback moth (Braun *et al.* 2004; Dosdall *et al.* 2011; Bahar *et al.* 2013; Noronha and Bahar 2018; Dancau *et al.* 2020), whereas other species are of minor importance. The impact of the two larval parasitoids on diamondback moth populations is considered high, but surveys conducted in western and eastern Canada showed that pupal parasitism by *D. subtilicornis* ranged only from 8% to 14% (Braun *et al.* 2004; Dancau *et al.* 2020).

Another species in the same genus, *Diadromus collaris* (Gravenhorst), is an important pupal parasitoid of diamondback moth in Europe and has been successfully introduced to many regions around the world for enhancing biological control of diamondback moth (Delvare 2004). However, it is currently not part of the existing parasitoid complex of diamondback moth in North America. The objective of this study was to conduct life table studies to determine the impact of *D. collaris* on diamondback moth populations in northwestern Switzerland, with the goal of providing baseline data from Europe, where *D. collaris* and *D. subtilicornis* co-exist. These data will assist evaluation of the potential impact of introducing an additional parasitoid, *D. collaris*, and possibly increase the overall pupal parasitism of diamondback moth in Canada.

Material and methods

Insect rearing

The original *P. xylostella* colony was provided by P. Hondelmann (Leibniz University, Hanover, Germany) and established in April 2014. Two generations were reared in the laboratory before colony specimens were used for experiments. Newly emerged moths were kept in gauze cages (Bugdorm-44590F; MegaView Science Co., Ltd., Taiwan) at 20 ± 1 °C and 60% relative humidity, with 16 hours light and were provided with honey and water every second day. White cabbage plants, *Brassica oleracea* Linnaeus (Brassicaceae), were placed inside the rearing cages and left overnight or up to 2 days for moth oviposition. These plants were then retrieved and transferred into separate rearing cages. New cabbage plants were

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added as additional food as needed. Newly emerged moths were collected with a mechanical aspirator (InsectaVac Aspirator; BioQuip Products, Rancho Dominguez, California, United States of America) and transferred back to the moth rearing cages.

Field sites and experimental design

The study was carried out at two locations in northwestern Switzerland each year from 2014 to 2016. One location was planted with conventional winter oilseed rape (*B. napus*) in the vicinity of Courroux, Canton Jura (47.363888°, 7.373627°). Due to regular crop rotation, oilseed rape was not planted in consecutive years, and therefore a new field was selected each year, preferably adjacent or close to the field sampled the previous year. Fields were sprayed with insecticide (thiacloprid, 0.4l/ha) against pollen beetle, *Brassicogethes aeneus* (Fabricius) (Coleoptera: Nitidulidae), before blooming in April but not during the exposure of sentinel plants. To prevent damage to the experimental oilseed rape fields (*e.g.*, trampling of plants), empty flowerpots were dug into the ground 1 m apart from each other along the edge of the field (first row). These were situated such that, once the pot containing the sentinel cabbage was placed into the pre-existing pot, the leaves would touch neither the ground nor any neighbouring plants.

A second location was at the Centre for Agriculture and Biosciences International, Switzerland, in Delémont, Canton Jura (47.3652°, 7.34367°). White cabbage seedlings, *B. oleracea*, as is normal practice in Switzerland, were planted in May of each year in a 20 × 6-m tilled plot, consisting of six rows one metre apart from each other. In each row, plants were placed every 0.5 m, but every second position was left unplanted to contain experimental plants (sentinels) within the plot. Plants were watered as needed. The plot was located near a forest edge and surrounded by natural wildflower meadows.

Assessment of mortality factors in different developmental stages of diamondback moth

To assess the mortality factors of diamondback moth and make data from Europe and Canada that were comparable, we used an experimental design for sentinel-based life tables that was similar to that described in Dancau *et al.* (2020). Laboratory-reared diamondback moth eggs, larvae, and pupae were exposed at each of the field plots at Courroux and Delémont on three- to six-week-old plants (5–8 true leaf stage, height *ca.* 20 cm) in each year from 2014 and 2016.

At each location, 7–12 sentinel plants infested with the designated life stage of the moth were placed into the field within the same month, but the exact dates depended on the availability of each larval instar. At the conventional winter oilseed rape location in 2015, every second flower pot was covered with a shelter composed of a 30 × 30-cm grey plastic roof supported by four wooden posts to investigate the effect of rain, which is thought to be a significant mortality factor of diamondback moth (Kobori and Armano 2003). Half of the plants infested with sentinel diamondback moth life stages were placed randomly under rain shelters, and the other half remained exposed. Some plants were randomly assigned to a cage treatment to assess background mortality of diamondback moth life stages when natural enemies were excluded. Cages were made of a wooden frame (60 × 30 × 30 cm, height × width × length) covered with fine mesh. The front side was closed with a taped Velcro seal to fully exclude predators and parasitoids. At the second location cabbage plot (Delémont), the same methods were used, except that plants were randomly distributed over the entire small field plot. After exposure, all plants were brought back to the laboratory, where individuals of each life stage were counted and moved into rearing containers to assess parasitism levels and additional mortality. All retrieved eggs, larvae, and pupae were reared in the laboratory and checked periodically for the emergence of parasitoids and diamondback moths. Voucher specimens of parasitoids have been deposited in the Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada).

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Eggs were obtained by placing up to six plants in large gauze cages (93.0 × 47.5 × 47.5 cm), each containing about 300 moths. Cabbage leaves ground in water produced a solution that was sprayed on the plants to stimulate moth oviposition. Cabbage plants were exposed to the moths overnight, and the following morning, eggs were counted using a light source and magnifying glass. Egg clusters laid on the stalk were removed with a paintbrush to avoid substantial overcrowding. The mean number of eggs per plant was 140 ± 7.83 (standard error; $N = 115$). Seven plants infested with eggs were exposed in the field plots during each trial, with three plants being covered, three plants remaining uncovered, and one caged control. Infested plants were exposed in the field plots at Courroux and Delémont for four days. After exposure, the plants were taken back to the laboratory, and first-instar larvae and any remaining eggs were counted.

First-instar larvae were obtained by infesting cabbage plants with eggs in the same way as described above, but the plants were maintained in the laboratory for 1–2 days at ambient conditions until first-instar larvae had hatched. The tiny larvae feeding inside leaf mines were counted using a portable digital microscope before exposure, and unhatched eggs were removed from the plants with a paintbrush. The average number of first-instar larvae per plant was 107 ± 4.27 (standard error; $N = 102$). Seven plants were exposed during each trial at each site, with three plants covered, three left uncovered, and one caged control. Sentinel plants infested with first-instar larvae were exposed to predation, parasitism, and abiotic conditions in the field for 3 ± 1 days, until the larvae reached the second-instar stage.

Second- and fourth-instar larvae were collected from the laboratory colony with a paint brush and were placed in clear plastic containers, each containing a cabbage leaf. Thirty larvae were placed on each sentinel plant after the plants were installed at Courroux and Delémont. To ensure that larvae were not lost during transport, groups of 30 larvae were transferred from the plastic containers to each sentinel cabbage plant after the plants were installed at Courroux and Delémont. Twelve plants were exposed at each site for each of these larval stages; of these plants, five were covered, five were left uncovered and two were caged as controls. Second-instar larvae were exposed for 6 ± 1 days, and re-collected as fourth-instar larvae, whereas fourth-instar larvae were exposed for 4 ± 1 days and re-collected as prepupae/pupae. Because a proportion of fourth-instar larvae might have left the plant to find suitable pupation sites elsewhere, we placed 20 additional plants in the field in 2015 and surrounded the rim of each flower pot with a sticky ring made of fly tape to trap any larvae leaving the plant.

Prepupae and pupae were obtained by transferring late fourth-instar larvae from the laboratory colony to new cabbage plants. Larvae were left on the plants for 24–48 hours until the majority of the larvae had reached the prepupal stage. The prepupae were counted, and the remaining fourth-instar larvae were removed before exposure. Twelve plants were exposed at each site for each of these stages; of these plants, five were covered, five were left uncovered, and two were caged as controls. Plants with sentinel pupae were exposed for 5 ± 1 days. The average number of pupae per plant was 21 ± 0.35 (standard error; $N = 213$).

In general, numbers of sentinel eggs, larvae, and pupae exposed in the field plots were likely substantially higher than naturally occurring densities would be; preliminary studies indicated that more realistic numbers, as used by Furlong *et al.* (2004), did not result in sufficient recovery to generate meaningful parasitism rates.

Construction of sentinel-based life tables

At Courroux, data were collected on sentinel diamondback moth stages twice each year (2014–2016) in the period from mid-May to the first week of July, which is shortly before the harvest of the oilseed rape fields. In the Delémont field plot, data were collected four times each year (in May, June, July, and August) in 2015 and 2016 and only a single time in 2014, the first year of the study (August 2014). Data collected in the first (May–June) and second

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halves (July–August) of 2015 and 2016 were pooled for both sites. Mortality rates were calculated indirectly from field data and applied to a hypothetical cohort of 1000 eggs in order to construct the life table. Because rainfall can be a significant source of larval mortality (Kobori and Armano 2003), we tried to measure mortality due to rainfall by adding a rain shelter treatment in 2015; however, the rain shelters were likely not effective, and diamondback moth mortality on sheltered and unsheltered sentinel plants did not differ significantly (Mann–Whitney rank-sum test; second-instar larvae, mean rank missing individuals: covered — 43.64, uncovered — 47.83, $U = 907.0$, $P = 0.448$, $N = 90$; fourth-instar larvae, mean rank missing individuals: covered — 45.26, uncovered — 45.79, $U = 992.5$ $P = 0.922$, $N = 90$; pupae, mean rank missing individuals: covered — 35.50; uncovered — 37.82, $U = 594.5$, $P = 0.637$, $N = 72$). Accordingly, mortality data from both treatments were combined for life table calculations, and the use of shelters was not continued in 2016. Potential mortality caused by rain is therefore included under "unknown mortality" in the life tables; this factor also includes biotic mortality factors such as pathogens and abiotic mortality factors such as temperature, wind, exposure, non-emergence, and unaccounted mortality between caged and uncaged treatments.

We assumed that sentinel eggs, larvae, and pupae that disappeared during the exposure period were lost due to predation or "unknown mortality". We subtracted the "unknown mortality" observed in the caged treatment from the mortality observed in the uncaged (exposed) treatment to estimate predation, assuming that missing individuals in the uncaged treatment were entirely lost due to predation. Because we could not exclude the possibility that a proportion of fourth-instar larvae may have left the plants to find suitable pupation sites, we calculated a correction factor from the average number of fourth-instar larvae caught on sticky rings surrounding the flower pods (13.7% ± 2.0% standard error; $N = 20$) and subtracted this value from the estimated predation rates, assuming that these larvae would have survived.

To estimate parasitism for each host life stage, we followed the calculations by Dancau *et al.* (2020), incorporating the numbers of individuals exposed, the numbers of individuals recovered, and the total numbers of individuals emerged (parasitoids + adult moths) into the calculation (Equation 1 in Dancau *et al.* 2020). This calculation included an estimate (correction) of parasitoid-induced mortality (*i.e.,* individuals that did not emerge) and of the numbers of parasitoids emerged. The estimate assumes that parasitism levels determined by numbers of parasitoids and moths that had emerged are the same for the individuals that were recovered but had died in the lab.

$$\text{Parasitism} = (((N_{\text{parasitoids emerged}}/N_{\text{moths+parasitoids emerged}}) \times N_{\text{recovered}})/N_{\text{exposed}}) \times 100\%, \quad (1)$$

where N equals the number of individuals.

All life tables referred to the fate of a hypothetical cohort of 1000 eggs. In the life tables, mortality attributable to infertility, parasitism, predation, and unknown factors was expressed as marginal attack rate, apparent mortality, real mortality, intensity of mortality (k-values), and generational mortality, following Bellows *et al.* (1992). Because we did not estimate the fecundity of *P. xylostella*, we used a literature value of 160 eggs (http://www.canolacouncil.org/canola-encyclopedia/insects/diamondback-moth/) to calculate the growth rates, being aware that fecundity can vary among *Brassica* species and even among cultivars (Zhang *et al.* 2012). The marginal attack rate (m_x) of a mortality factor is the proportion of individuals of a particular stage that would be attacked by a single factor acting alone in the system (Bellows *et al.* 1992). When mortality factors are acting sequentially and without other contemporaneous mortality factors, the marginal attack rate (m_x) equals the apparent mortality (q_x). When factors are acting simultaneously, the marginal attack rate (m_x) is calculated as $m_x = 1 - (1 - d_x)\, d_s/d_x$, where d_s is the observed mortality by a single mortality factor and where d_x is the mortality from all causes combined in one life stage interval, assuming that each contributes equally to mortality. The apparent mortality (q_x) is the

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fraction of those individuals entering a specific stage (l_x) that die in that same stage or the fraction of those subjected to a mortality factor that die as a result of that factor. Apparent mortality was calculated from the exposure experiments described above, using the number of dead (missing) or parasitised individuals (d_x) recorded from each life stage (x) of diamondback moth; that is, $q_x = d_x/l_x$. Total mortality of each life stage was the sum of the percent mortality from all mortality factors combined. Information on the population dynamics of diamondback moth is given by the net reproductive rate of increase (R_0), which shows the number of times the population increases or decreases from one generation to the next (Van Driesche *et al.* 2008). Growing populations have R_0 values greater than 1, whereas R_0 values less than 1 indicate that the population is declining. R_0 was calculated from the realised progeny divided by the number of eggs in the first generation ($l_x = 1000$).

Results

Parasitism and species composition

Between 2014 and 2016, seven primary parasitoid species and one hyperparasitoid were associated with diamondback moth in northwestern Switzerland (Table 1). Eggs were rarely parasitised by *Trichogramma* sp. (Hymenoptera: Trichogrammatidae). The most abundant larval parasitoids were *Diadegma fenestrale* (Holmgren) and *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae), with parasitism as high as 48% (*D. fenestrale*, Courroux, May–June 2015) and 23% (*D. semiclausum*, Delémont, July–August 2015; Table 1). Occasionally *Diadegma* spp. were hyperparasitised by *Mesochorus* sp. (Hymenoptera: Ichneumonidae), but hyperparasitism did not exceed 2% at any one site or time. The solitary larval parasitoid *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae) was found only sporadically. Pupae were attacked mainly by *Diadromus collaris* and less frequently by *Diadromus subtilicornis*. Parasitism by *D. collaris* reached nearly 30% in Courroux in 2014, whereas parasitism by *D. subtilicornis* was less than 5% in all years and sites. On a single occasion (May 2015), nearly 18% of sentinel pupae were exclusively parasitised by the generalist pupal parasitoid, *Itoplectis maculator* (Fabricius) (Hymenoptera: Ichneumonidae). Cumulative parasitism rates varied greatly between exposure periods, ranging from 19% to 64% (mean: 45% ± 6% standard error; Table 1).

Mortality factors, generational mortality, and reproductive rates of diamondback moth

Recovery of all stages of diamondback moth was significantly higher in caged than in uncaged treatments (Mann–Whitney test: $P < 0.0001$ for eggs ($N = 129$), second- and third-instar larvae ($N = 222$), and fourth-instar larvae ($N = 202$); $P = 0.001$ for first-instar larvae ($N = 107$); $P = 0.003$ for pupae ($N = 211$). Mortality in the egg and first-instar larval stages (shown as apparent mortality in Table 2 and Supplementary material, Tables S1–8) was highest due to unknown factors, averaging 35.6 ± 5.8 (standard error) and 30.2 ± 6.7 (standard error) individuals, respectively ($N = 8$ life tables). In all following stages (second- and third-instar larvae, fourth-instar larvae, and pupae), the most important mortality factor was predation, averaging 42.7% ± 4.6%, 37.5% ± 4.2%, and 21.6% ± 5.7% (standard error) individuals, respectively. Parasitism was the highest in the second- and third-instar larval and pupal stages, averaging 13.6% ± 2.3% and 15.3% ± 4.0% (standard error), respectively.

In seven out of eight life tables (one for each growing season month at each location), mortality of combined second- and third-instar larvae was the largest contributor to *generational mortality* (range: 29.5%–50.3%, mean 39.2% ± 2.5%, $N = 8$; Table 3; Supplementary material, Tables S1–8), and for only one sentinel generation was egg mortality (31.5%) which is the most important factor (Supplementary material, Table S7). The contribution of pupal mortality to generational mortality

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Table 1. Cumulative percent parasitism (number of individuals) by parasitoids (Hymenoptera) in sentinel-based life tables for diamondback moth, *Plutella xylostella*, at two locations, Courroux and Delémont, Switzerland.

		Delémont					Courroux		
		2014	2015			2016	2014	2015	2016
Parasitoid	Host Stage	August	May/June	July/August	May/June	July/August	June/July	May/June	May/June/July
Trichogrammatidae									
Trichogramma sp.	Egg	0.07 (1)	0	1.26 (43)	0	0	0.09 (2)	0	0.46 (10)
Braconidae									
Cotesia vestalis (Haliday)	Larval	0	0	0	1.42 (7)	0.81 (3)	0	0	0.82 (5)
Ichneumonidae									
Diadegma fenestrale (Holmgren)	Larval	0	31.68 (174)	0	13.39 (66)	15.16 (64)	12.97 (21)	48.21 (162)	13.9 (101)
Diadegma semiclausum (Hellén)	Larval	16.09 (31)	12.42 (71)	23.2 (185)	1.21 (6)	14.41 (64)	11.91 (16)	1.01 (4)	13.09 (92)
Mesochorus sp.	Hyperparasitoid	0	0.18 (1)	0	0	0	0	1.58 (6)	0.98 (6)
Diadromus collaris (Gravenhorst)	Pupal	21.78 (55)	2.08 (5)	1.26 (7)	0	25.11 (90)	29.84 (86)	10.27 (29)	4.07 (21)
Diadromus subtilicornis (Gravenhorst)	Pupal	0	0	0	2.99 (11)	0	2.78 (8)	0	4.07 (21)
Itoplectis maculator (Fabricius)	Pupal	0	17.86 (43)	0	0	0	0	0	0
Total cumulative % parasitism		37.94	64.22	25.72	19.01	55.49	57.59	61.07	37.39

Table 2. Summary of apparent mortality (the ratio of the number of individuals dying in a stage to the number entering the stage), total mortality, and population growth (R_0) of diamondback moth, *Plutella xylostella*, populations at two locations, Courroux and Delémont, Switzerland, 2014–2016. For life table details, see Supplementary material, Tables S1–8.

		Courroux			Delémont				
		2014	2015	2016	2014	2015		2016	
Host stage		June/July	May/June	May/June/July	August	May/June	July/August	May/June	July/August
Egg									
	Predation	0.2617	0.3379	0.3339	0.4600	0.4423	0.5310	0.1736	0.2154
	Unknown	0.5960	0.4599	0.2712	0.2415	0.0749	0.3216	0.5033	0.3761
	Infertility	0.0046	0.1345	0.0185	0.0239	0.3781	0.0135	0.0178	0.0132
	Parasitism	0.0009	0.0000	0.0046	0.0007	0.0000	0.0343	0.0000	0.0000
Larva 1									
	Predation	0.2357	0.2870	0.0129	0.3922	0.2262	0.2883	0.1811	0.4293
	Unknown	0.5028	0.1856	0.4167	0.3314	0.5738	0.1954	0.2025	0.0056
	Parasitism	0.1743	0.2818	0.0159	0.0112	0.0711	0.1001	0.0000	0.0052
Larva 2–Larva 3									
	Predation	0.6817	0.3383	0.4518	0.2792	0.3467	0.3807	0.3950	0.5394
	Unknown	0.2733	0.4667	0.3222	0.6000	0.3333	0.4815	0.1667	0.1889
	Parasitism	0.0397	0.1502	0.1899	0.0375	0.2416	0.1172	0.1029	0.2093
Larva 4									
	Predation	0.5241	0.3863	0.2991	0.2874	0.3763	0.5430	0.1913	0.3930

(*Continued*)

Table 2. (*Continued*)

		Courroux			Delémont				
		2014	2015	2016	2014	2015		2016	
Host stage		June/July	May/June	May/June/July	August	May/June	July/August	May/June	July/August
	Unknown	0.2600	0.3500	0.3526	0.2333	0.1833	0.2778	0.3330	0.2400
	Parasitism	0.0348	0.0760	0.0821	0.1122	0.1300	0.0147	0.0574	0.0893
Prepupa/pupa									
	Predation	0.2382	0.4158	0.1770	0.3360	0.0820	0.4129	0.0423	0.0198
	Unknown	0.0270	0.0000	0.0741	0.0345	0.0000	0.0230	0.0147	0.0930
	Parasitism	0.3262	0.1027	0.0813	0.2178	0.1994	0.0126	0.0299	0.2511
Total mortality		99.9998	99.9966	99.9340	99.9543	99.9882	99.9961	98.7946	99.8781
R_0		0.00004	0.00539	0.10555	0.07318	0.01889	0.00619	1.92859	0.19501

Table 3. Contribution (%) of each mortality factor to the generational mortality ($100k_x/K_G$) of diamondback moth, *Plutella xylostella*, populations at two locations, Courroux and Delémont, Switzerland, 2014–2016. For life table details, see Supplementary material, Tables S1–8.

	Courroux			Delémont				
	2014	2015	2016	2014	2015	2016		
Stage	June/July	May/June	May/June/July	August	May/June	July/August	May/June	July/August
Egg								
Predation	4.92	10.57	7.96	11.78	14.97	14.55	8.00	5.50
Unknown	11.20	14.39	6.46	6.19	2.53	8.81	23.21	9.61
Infertility	0.01	0.11	0.21	0.15	0.63	0.02	0.25	0.18
Parasitism	0.00	0.00	0.05	0.00	0.00	0.04	0.00	0.00
Σ	16.13	25.08	14.68	18.12	18.14	23.42	31.46	15.30
Larva 1								
Predation	5.14	5.79	0.26	10.17	7.15	4.63	6.17	9.42
Unknown	10.96	3.74	8.34	8.60	18.13	3.14	6.90	0.12
Parasitism	3.80	5.68	0.32	0.29	2.25	1.61	0.00	0.11
Σ	19.90	15.21	8.92	19.06	27.52	9.37	13.06	9.65
Larva 2–Larva 3								
Predation	29.29	11.92	23.56	10.87	12.86	16.15	17.53	26.57
Unknown	11.74	16.44	16.80	23.36	12.37	20.42	7.40	9.31
Parasitism	1.71	5.29	9.90	1.46	8.96	4.97	4.57	10.31
Σ	42.74	33.66	50.27	35.69	34.19	41.54	29.49	46.19
Larva 4								
Predation	8.92	8.62	8.16	6.53	8.58	12.54	7.74	11.60
Unknown	4.42	7.81	9.62	5.30	4.18	6.42	13.47	7.09
Parasitism	0.59	1.70	2.24	2.55	2.96	0.34	2.32	2.64
Σ	13.93	18.13	20.02	14.39	15.72	19.30	23.53	21.33
Prepupa/pupa								
Predation	2.94	6.35	3.25	7.28	1.29	5.86	1.19	0.41
Unknown	0.33	0.00	1.36	0.75	0.00	0.33	0.42	1.92
Parasitism	4.03	1.57	1.49	4.72	3.14	0.18	0.85	5.20
Σ	7.30	7.92	6.11	12.74	4.44	6.36	2.46	7.53

was the lowest among all stages, ranging from 2.5% to 12.7% (mean 6.9% ± 1.1% standard error, $N = 8$). Accordingly, the contribution of pupal parasitism was 2.7% ± 0.7% on average, with a maximum of 5.2%.

In oilseed rape fields near Courroux, total mortality for the sentinel-based life tables was 99.99% in 2014 and 2015 and 99.93% in 2016. In the experimental cabbage plots at Delémont, the situation was similar. Total mortality in May–June was 99.99% and 98.80% in 2015 and 2016, respectively (Table 2; Supplementary material, Table S1). In the second half of the summer, total mortality was 99.95%, 99.99%, and 99.88% in the three years of the study, respectively. Accordingly, the net reproductive rates (R_0) calculated for seven out of eight life

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tables was less than 1, indicating declining populations in those years (Table 2). Only in May–June 2016 did R_0 equal 1.93 in the cabbage plot at Delémont, indicating slightly growing populations.

Discussion

In importation biological control, life table studies in the native range of an insect pest are an important tool to identify potential biological control agents that impact the pest's generational mortality, assuming that the impact in the invaded range would be similar if the agent were introduced (Haye *et al.* 2010; Jenner *et al.* 2010; Gillespie *et al.* 2019). In addition, life tables in the introduced range can help to identify the life stages of the pest during which additional mortality — for example, due to the release of an exotic natural enemy — could significantly reduce population growth (Toepfer and Kuhlmann 2006; Haye *et al.* 2014). Ideally, life tables are conducted in both the native and the introduced ranges to evaluate if the introduction of a given biological control agent could have substantial impact on the target. Following this approach, multiple decrement life tables show that the introduction of the European parasitoid *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae) into canola-growing regions of Canada would have the potential to substantially reduce populations of the invasive cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) (Gillespie *et al.* 2019).

Life tables for diamondback moth field populations have been conducted in several parts of the world, including in Australia, Canada, and Brazil (Furlong *et al.* 2004; Dancau *et al.* 2020; Farias *et al.* 2020), but little is known about the mortality factors regulating diamondback moth populations in Europe. In this study, the extremely low net reproductive rates found in seven out of eight life tables ($R_0 < 1$) suggest that diamondback moth populations in Switzerland are mostly driven by immigration and recolonisation. The phenology of diamondback moth in Switzerland is not well known, but monitoring data from Stetten, Canton Aargau, Switzerland indicate that this species occurred in May of each of the study years (calendar weeks 19–22 in 2014 to 2016) and was present until the end of September (C. Sauer, personal communication). It is assumed that diamondback moth can develop three to five generations in a year, but mass outbreaks are believed to result from wind migration (Balmelli *et al.* 2012).

Although many *Trichogramma* spp. are known to develop successfully on diamondback moth eggs (Tabone *et al.* 2010), egg parasitism never exceeded 2% and was not a key factor in regulating diamondback moth populations in this study. As in many other parts of the world (Sarfraz *et al.* 2005), larval parasitoids in the genus *Diadegma* played a major role at our study sites. Our results confirmed an earlier study by Juric *et al.* (2015), which reported two species, *Diadegma semiclausum* and *D. fenestrale*, as being abundant in Switzerland. Temporally, both species overlapped, with *D. fenestrale* being the more abundant species in the first half of the summer and *D. semiclausum* becoming the more abundant species towards the end of the summer. Because many parasitised sentinel larvae may have been lost in this study due to predation, abiotic factors, and active movement from the test substrates, it remains difficult to estimate accurately the real larval parasitism levels in natural diamondback moth populations. As shown by Juric *et al.* (2015), molecular markers may be a more precise tool for detecting *D. fenestrale* and *D. semiclausum* in field-collected larvae, as larvae can be processed immediately and mortality during rearing is not a factor. Juric *et al.*'s (2015) study in Switzerland found that larval parasitism by these two species was 72.2%, suggesting that larval parasitism could be much higher than the present study determined. In contrast, parasitism estimates for pupae are likely more realistic, since to a certain degree, pupae are protected from predators and abiotic factors by their surrounding cocoons.

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Because pupal parasitism of diamondback moth in North America is generally low (Shelton *et al.* 2002), the introduction of an additional exotic parasitoid has been considered as a way to increase suppression of diamondback moth populations. One obvious candidate for introduction would be the solitary endoparasitoid, *D. collaris* — the dominant pupal parasitoid in this study — which is widely distributed throughout the Palaearctic region from Europe to Japan and China and is also present in South Africa. To date, the known host range of *D. collaris* in Europe is limited to three species: diamondback moth, European grapevine moth, *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae) (Meyer 1934; Telenga 1934), and leek moth, *Acrolepiopsis assectella* (Zeller) (Lepidoptera: Glyphipterigidae) (Lecomte 1977). In areas of Europe where it occurs, *D. collaris* is believed to overwinter in the adult stage (Valemberg and Valo 1974). Its entire life cycle (egg to adult) lasts only 14.5 days at 22.5 °C (Wang and Liu 2002), enabling *D. collaris* to produce several generations per year. Its mean oviposition period lasts 11.5 ± 1.8 days at 25 °C, and in laboratory studies, the synovigenic females were able to parasitise 43.7 ± 5.2 pupae on average, with approximately 96% adult emergence (Liu *et al.* 2001). In addition, *D. collaris* was also observed to feed on its host's haemolymph to supplement nutrition (Lloyd 1940; Sakanoshita *et al.* 1987), a behaviour that could have added to the (low) unknown pupal mortality observed in this study (Abram *et al.* 2019). First imported from England to New Zealand in the 1930s for enhancing biological control of diamondback moth, *D. collaris* has since been successfully introduced to Australia, Indonesia, and Malaysia (Delvare 2004; Furlong *et al.* 2013). The second pupal parasitoid found in this study, *D. subtilicornis*, is already present in North America and is assumed to be more abundant in northern regions of Europe, including in Poland, Finland, and Russia (Delvare 2004). The present study determined that pupal parasitism by *D. subtilicornis* ranged from 0% to 4%, or the species was completely absent. In comparison, parasitism by *D. subtilicornis* in Ontario, Canada was approximately 10% (Dancau *et al.* 2020). In this study, pupal parasitism by *D. collaris* was 20%–30% in some of our exposures, confirming its potential for biological control. Since generational mortality was mainly driven by abiotic ("unknown") mortality factors and predation of small second- and third-instar larvae, the overall contribution of pupal parasitoids was low (< 6%).

In comparison, the contribution of pupal parasitoids to generational mortality in Ontario was even lower, reaching only 1%–3% (Dancau *et al.* 2020). However, because generational mortality of diamondback moth under current conditions in Ontario is mainly driven by predation of larvae and because diamondback moth populations are declining ($R_o < 1.0$), the introduction of *D. collaris* to Ontario would likely have negligible effects. In other regions of Canada, such as Prince Edward Island, where diamondback moth may have increasing populations ($R_o > 1.0$) and low larval mortality, the addition of *D. collaris* may be more promising. Life table data from different regions of Canada could help to predict where the introduction of *D. collaris* on diamondback moth populations would have important impact, as was demonstrated for the cabbage seedpod weevil, *C. obstrictus* (Gillespie *et al.* 2019). Furthermore, if *D. collaris* is deemed to be a potential candidate for introduction in Canada, host range and competitive interaction studies are needed to assess the ecological safety of such an introduction.

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