EFFECT OF *COTESIA RUBECULA* (HYMENOPTERA: BRACONIDAE) ON SURVIVAL OF LARVAL COHORTS OF *PIERIS RAPAE* (LEPIDOPTERA: PIERIDAE) ON COLLARDS: EVALUATION OF AN INTRODUCED BIOLOGICAL CONTROL AGENT

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Abstract

Survival of artificial cohorts of larvae of the imported cabbageworm, *Pieris rapae* (L.), was assessed in a collard (*Brassica oleracea* L., var. *acephala*) patch on an organic vegetable farm in western Massachusetts. We recorded a significant drop in survival of larvae between the 4th and 5th instar due to parasitism by the parasitoid *Cotesia rubecula* (Marshall), which was introduced to New England from China in 1988. This was a large change from the survivorship pattern of *P. rapae* observed in the same area in 1985-1986, in which there was a significant drop in survival between 5th instars and pupae due to *Cotesia glomerata* (L.), the dominant parasitoid of *P. rapae* in New England at the time. In our study, parasitism by *C. rubecula* averaged 62.4 ± 8.6%, while no parasitism by *C. glomerata* was observed. The introduction of *C. rubecula* is now very likely to be benefitting organic vegetable producers in western Massachusetts, killing more larvae and at an earlier life stage than the previous parasitoid, reducing the potential for damage to cole crops.

Key Words: biological control, parasitoid displacement, imported cabbageworm, effectiveness *Cotesia glomerata*

Resumen

La supervivencia de cohortes de larvas del gusano del repollo, *Pieris rapae* (L.), establecidas artificialmente en plantas de col (*Brassica oleracea* L., var. *acephala*), fue evaluada en una finca productora de vegetales orgánicos en el oeste de Massachusetts. Registramos una reducción en la supervivencia de larvas entre el 4to y 5to instar, causado por el parasitismo del agente de control biológico *Cotesia rubecula* (Marshall), el cual fue introducido al estado de Nueva Inglaterra proveniente de China en 1988. Se observó un cambio considerable en el patrón de supervivencia de *P. rapae* con respecto a lo registrado en un estudio previo entre 1985-1986 en la misma area, en el cual se encontró una reducción de la supervivencia en el 5to instar y el estado pupal causado por *Cotesia glomerata* (L.), el parasitoide dominante de *P. rapae* en Nueva Inglaterra en ese momento. En nuestro estudio el parasitismo por *C. rubecula* promedio 62.4 ± 8.6%, mientras que no se observó parasitismo por *C. glomerata*. Estos resultados muestran que la introducción *C. rubecula* probablemete está beneficiando a los agricultores orgánicos de vegetales en el oeste de Massachusetts, eliminando más larvas y cuando estas son más pequeñas con respecto al parasitoide establecido anteriormente, reduciendo así el potencial de daños significativos a cultivos de coles.

Palabras Clave: control biológico, desplazamiento de parasitoides, gusano importado del repollo, eficacia, *Cotesia glomerata*

The imported cabbageworm, *Pieris rapae* (L.) (Lepidoptera: Pieridae), is an invasive pest of *Brassica* crops in North America, Australia, and New Zealand (Jones et al. 1980). In the United States, 2 biocontrol agents have been released against *P. rapae* larvae during different historical periods, to reduce feeding damage to an acceptable level to growers.

The gregarious parasitoid *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) was released in 1884 near Washington, D.C. (Clausen 1978). *Cotesia glomerata* parasitizes first and second instars of *P. rapae*, and kills *P. rapae* larvae at the end of the fifth instar, after most *P. rapae* larval feeding has occurred, so that parasitism usually does little to reduce within generation *P. rapae* damage. Indeed larvae parasitized by *C. glomerata* generally consume more food than unparasitized larvae during their development (Rahman 1970), although this varies with parasitoid brood size (Harvey 2000).

The second introduced larval parasitoid was *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae), a solitary, host-specific parasitoid. Introductions of this species occurred from 1960 to 1992 (Puttler et al. 1970; Williamson 1971 & 1972; Parker & Pinnell 1972; McDonald & Kok 1992; Lee & Heimpel 2005; Wold-Burkness et al. 2005). In 1988, releases of a Chinese strain of this species were made at 17 different locations in New England (Van Driesche & Nunn 2002). Like *C. glomerata*, *C. rubecula* attacks first and second instars of *P. rapae*, but kills fourth instars, before most feeding has occurred (Le Masurier & Waage 1993). Total feeding per larva is greatly reduced since 85% of feeding occurs in the last instar (Parker & Pinnell 1973) and final weight of *C. rubecula*-parasitized larvae is only 5-10% of that of mature healthy 5th instars (Harvey et al. 1999).

Furthermore, from an intergenerational perspective, while direct comparisons of rates of parasitism by these 2 *Cotesia* species are few, in a recent regional survey in the northern United States and Canada (Herlihy et al. 2012), average rates of parasitism were higher ($47 \pm 3\%$ [95% CI, $n = 1041$]) for *C. rubecula* than *C. glomerata* ($25 \pm 3\%$ [95% CI, $n = 641$]), across 32 sites, with sites being dropped for each species if it was not present. Recoveries of these species in this survey were nearly all disjunct and *C. rubecula* has largely replaced *C. glomerata* in the United States above latitude N 38° 48', indicating that it is the superior competitor in that region (Herlihy et al. 2012). Such displacement, not the focus of this study, likely results from both intrinsic superiority of *C. rubecula* larvae (which are mandibulate and kill the non-mandibulate *C. glomerata* larvae in cases of co-parasitism) (Laing & Corrigan 1987) and behavioral traits that enable *C. rubecula* wasps to more efficiently find and exploit *P. rapae* (Cortesero et al. 1997). High rates of parasitism of *P. rapae* larvae in organic vegetation farms in western Massachusetts are now the norm, averaging 75% in both spring (Van Driesche 2008) and fall (Van Driesche unpub.) (Fig. 1).

Our study goal was to quantify the effects of *C. rubecula* on survivorship of *P. rapae* larval cohorts, using cage exclusion methods, and to compare the current survivorship pattern to that observed in western Massachusetts in the mid-1980s (Van Driesche 1988), when *C. glomerata* was the only important larval parasitoid of *P. rapae*. We predicted that (1) *C. rubecula* would be the dominant parasitoid because it has largely displaced *C. glomerata* in the study region (Van Driesche 2008; Herlihy et al. 2012), (2) rates of parasitism would be high, given the generally high levels of this species in earlier state surveys, and (3) survival of *P. rapae* larvae would decrease sharply from the fourth to fifth instar.
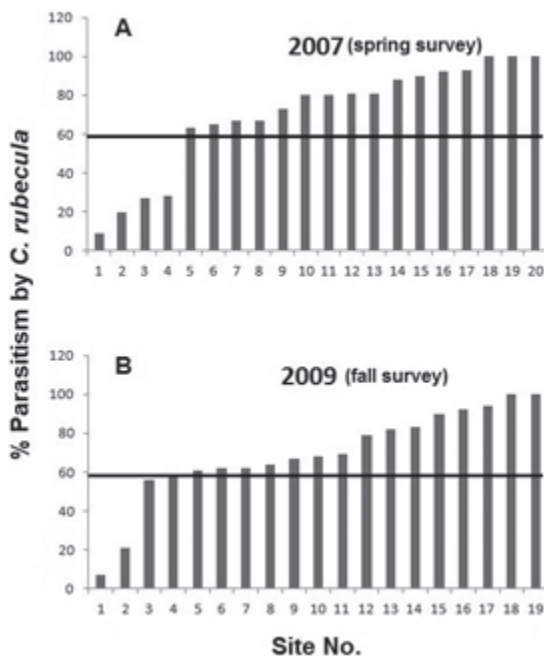

Fig. 1. Distribution of parasitism rates by *Cotesia* spp. among organic vegetable farms in western Massachusetts in spring 2007 (data redrawn from Van Driesche (2008) and survey data of fall 2009, where the horizontal line is level of parasitism at site for cohort study in 2011. (Site numbers do not correspond between surveys.)

MATERIALS AND METHODS

Massachusetts *Cotesia rubecula* Parasitism Surveys

A survey *Cotesia* parasitism of *P. rapae* larvae in organic vegetable farms or private gardens in western Massachusetts was conducted in fall of 2009, using the same protocols as a survey in the same region in spring of 2007 (Van Driesche 2008). In brief, 19 organic vegetable farms or gardens in the four western counties of Massachusetts were visited, and the cole crops present (cabbage, collards, broccoli, Brussels sprouts) were examined. The survey was conducted from 10 Sept to 22 Oct of 2009, and all *P. rapae* larval stages, pupae, emerged pupae, parasitoid cocoons (live or emerged) on plants were collected, until at least 30 individuals had been located. These were then taken to the laboratory and dissected. Parasitism by *C. rubecula* or *C. glomerata* was determined based on detection and recognition of parasitoid eggs or larvae in dissected host larvae, together with the number of parasitoid cocoons (live or emerged) found during the field search. Parasitized larvae plus parasitoid cocoons (live or emerged) formed the parasitized group, which was divided by the count of all host or parasitoid

stages collected to calculate the rate of parasitism (all other details as in Van Driesche [2008]). For *C. glomerata* cocoons, one group of cocoons was counted as one, since it represents one parasitized host.

Study Location

In June of 2011, 130 collard seedlings were planted at an organic vegetable farm (Intervale Farm in Westhampton, Massachusetts, 42°17.41'N, 72°46.19'W) to form an experimental plot where the interaction of *C. rubecula* and *P. rapae* larvae could be studied. Seedlings were planted in 6 rows of about 22 plants each, at 50 cm intervals. The land used for the patch had not been planted previously with cole crops, and was used the previous year for corn. In 2011, the area around the patch was planted to cole crops, corn, beans, and tomatoes. Neither the study patch nor the surrounding area were treated with pesticides during 2011.

Plants

Before each of 4 experiments, groups of 70 large collard plants (c. 30 cm tall with 7-10 leaves) in 15 cm dia pots were purchased from Harvest Farm in Whately, Massachusetts, where they had been grown in greenhouses without pesticides. After purchase, plants were held for about 1 week in the laboratory and watered daily until used in the experiment. Two days before starting an experiment, plants were taken to the field plot to acclimatize to outdoor conditions. Potted plants were placed within the existing rows between soil-grown collard plants; there were 15 potted plants in each of the plot's 4 rows (which were used for the main treatments) and 10 potted plants in a fifth row (with larvae needed to determine the accuracy of visual estimation of parasitism rates). Pots were set into evenly spaced shallow holes dug in the ground to help conserve moisture and prevent pots from blowing over, and were watered every other day during the experiment.

Insect Rearing, Handling, and Inoculation of Experimental Plants

Pieris rapae larvae used came from a laboratory colony initiated with butterflies collected at local sites near Amherst, MA, in 2010 and reared on collards. Butterflies were provided with sugar solution ("Instant Hummingbird Nectar," Perky Pet Woodstream Corp. Lititz, PA) and allowed to oviposit on collard seedlings. After egg hatch, larvae were reared on seedling collards until just beyond the neonate stage (e.g., having taken their first meal and turned from yellow to green due to food in their guts). Young 1st instars were then

taken, along with plants, to the field site where larvae were placed on the experimental plants using a paintbrush dipped in nectar water (sugar induces plant acceptance by neonates). Five 1st instars were placed on each potted plant.

Experimental Design

We tested the effects of 4 levels of natural enemy exclusion on survival of our cohorts of *P. rapae* larvae: (1) no exclusion (uncaged plants without Tanglefoot [Contech Enterprises Inc. Victoria, BC, Canada] on pots), (2) full exclusion (plants inside net sleeves and with Tanglefoot on pots), and (3, 4) 2 levels of partial exclusion, being either with sleeves and no Tanglefoot, or the reverse. There were 15 plants (replicates) for each level of exclusion and each plant was considered an experimental unit. Treatments were placed within their own rows, with all 15 plants arranged in one row, but immediately next to (< 0.5 m) a similar row of plants for treatments 2, 3, and 4. The maximum distance between pots of different treatments was 1.5 m. The experiment was repeated 4 times (Jul, Aug, Sept and Oct) to determine if important seasonal variation existed, as suggested by the slightly higher levels of *C. glomerata* parasitism in a fall survey vs. spring survey in Massachusetts (Van Driesche unpub. [Fall] vs. Van Driesche 2008 [Spring]). The same plot was used for all 4 runs of the experiment, but in each run, treatments were assigned to different rows.

In 2 of the 4 treatments, Tanglefoot was applied to pots to prevent walking predators from moving up the pots from the soil onto the plants. Tanglefoot was painted once in a band around the outsides of each pot in this treatment at the beginning of the experiment. For 2 of the 4 treatments, organdy sleeves were placed over the entire plant to exclude flying predators and parasitoids. Sleeves were held slightly away from the foliage of the potted plants by 4 stakes driven into the ground around each pot; sleeves were fitted over the stakes, dropping to the mid-pot level (about 5 cm above soil level). The bottom edges of the sleeves were left loose and were not secured to pots in order to facilitate sleeve removal, which was needed for frequent counting of larvae and watering of plants.

During insect counts, parasitism was estimated visually (based on shift in caterpillar color from green to whiter tones and visible shapes of parasitoids larvae in caterpillars) as soon as parasitism could be detected; however, these putatively parasitized larvae were left on plants for continued observation. To determine the relationship between visual estimates of parasitism and the real rates of parasitism (as would have been seen in dissection if larvae were removed and killed), in the fifth row we placed ten additional potted plants without organdy bags or Tanglefoot. Larvae in this group were placed on plants at the

same time and in the same manner as for the cohorts of the main experiment. When larvae in the cohorts reached the fourth instar, we conducted a visual estimate of parasitism in the same manner as for the main experiment. We then checked our visual estimate by dissecting these extra larvae in the laboratory, using the same characters for species recognition as described in Herlihy et al. (2012). The comparison of parasitism rates of these larvae via field visual assessments and their subsequent dissection in the laboratory allowed us to measure the accuracy of our visual assessments of parasitism in the main experiment.

Data Collection

We counted surviving *P. rapae* larvae on all potted plants at a series of time points from first instars to pupae. Larval survival was checked visually in the field by examining potted plants leaf by leaf, recording all living larvae (by instar) and any parasitoid cocoons. For treatments in which plants were covered with organdy sleeves, these were lifted up to examine plants and then replaced. If any wild *P. rapae* eggs were found on unsleeved experimental plants, they were removed. During the first 2 runs (7-20 Jul and 4-16 Aug), plants were examined every second day, providing 6 observations per run. During the last 2 runs (3-24 Sept and 27 Sept to 17 Oct), the plants were initially examined every second day, but larvae developed more slowly due to lower temperatures and therefore after the first 2 observations the period between observations was changed to every third day, providing 7 observations in run 3 and 8 in run 4.

When the surviving larvae of a cohort reached the fourth instar, each larva was assessed visually in the field and classified as parasitized or not, by either *C. rubecula* or *C. glomerata*. (Parasitism by this stage was visible due to a change in body color and parasitoid species was recognized by larval size and appearance, changes which were familiar to us from rearing both parasitoids in the laboratory).

Life Table Construction

Life tables were constructed for cohorts of larvae from treatment groups within each monthly run of the experiment, but only 4 life tables (one per treatment, pooled over months) are presented. We used the marginal rate equation $m_B = d_B/(1-m_A)$, where m_B is the marginal attack rate of the parasitoid, d_B is the death rate from parasitism, and m_A is the marginal attack rate for predation (here, disappearance), to calculate the underlying rates of parasitoid attack from the observed rates of parasitism and disappearance for fourth instars in life tables (the only stage with 2 observed mortality factors) (Elkinton et al. 1992).

Statistical Analyses

All statistical analyses were conducted using the program R (version 2.13.1). For *P. rapae* stage survival, analyses were based on insect counts (of particular stage) per plant, while for parasitism, data were proportions (of fourth instars) parasitized. Parasitism data were arcsine transformed in order to meet the assumption of normality. Number of survivors for selected *P. rapae* life stage and rates of parasitism were compared across run dates (month). Rates of parasitism were compared using a t-test for treatments with and without sleeves. Survival data were analyzed with an ANOVA, followed by a Tukey HSD test.

RESULTS

Rates of *C. rubecula* Parasitism in Regional Surveys

The rate of *C. rubecula* parasitism observed in the 2011 cohort survival experiment study (59-60% apparent parasitism [Table 1]) was typical of

TABLE 1. NUMBER OF LARVAE REACHING DESIGNATED LIFE STAGES AND RATES OF *COTESIA RUBECULA* PARASITISM FOR *PIERIS RAPAE* LARVAL COHORTS SUBJECTED TO DIFFERENT LEVELS OF NATURAL ENEMY EXCLUSION, IN AN EXPERIMENTAL COLLARD FIELD IN WESTAMPTON, MASSACHUSETTS (POOLED OVER FOUR EXPERIMENTAL MONTHS [JUL-OCT, 2011]).

	No.[1] of larvae surviving to		% Parasitism[2]	
	5th instar	Pupae	Apparent rate (n)	Marginal rate
S (-), TF (-)[3]	15 a[4] (5%)	11 a (3.7%)	59 aA (68)	72 aA
S (-), TF (+)	16 a (5.3%)	9 a (3%)	60 aA (75)	73 aA
S (+), TF (-)	102 b (34%)	82 b (27.3%)	4 bB (129)	5 bB
S (+), TF (+)	136 b (45.3%)	109 b (36.3%)	1 bB (146)	1 bB

[1]Number of 300 original first instars surviving to stage.
[2]Parasitism rates measured when host cohorts reach the fourth instar
[3]Treatments: S = sleeved, TF = tangle foot; - is without this type of exclusion; + is with the type of exclusion
[4]Differing lower case letters denotes statistically significant differences within columns (Tukey HSD test). Differing upper case letters denotes statistically significant differences within rows (Tukey HSD test) (for parasitism only).

those seen in surveys under similar conditions in western Massachusetts in spring of 2007 and fall of 2009 (Figs. 1A and 1B), which together covered 39 locations. In the spring 2007 survey, 16 of 20 sites had *C. rubecula* parasitism rates equal or higher than the 2011 cohort study site, and in the fall 2009 survey, 17 of 19 sites did so. This indicates that results from our detailed cohort study are representative of results across western Massachusetts.

Survival of *P. rapae* Cohorts

A 3-factor (month, sleeves, and Tanglefoot) factorial ANOVA showed that month of exposure had no significant effect on survival to fifth instar (F = 0.17; df = 3; P = 0.92) or survival to pupa (F = 0.05; df = 3; P = 0.83). Therefore, in further analyses, data were pooled across months to explore differences among the 4 levels of natural enemy exclusion.

In a 2-factor (sleeves and Tanglefoot) factorial ANOVA, differences in the survival of experimental cohorts to the pupal stage with sleeves (presence vs. absence) and Tanglefoot (presence vs. absence) as factors were highly significant (ANOVA, F = 63.2; df = 3; P < 0.0001). Survival of cohorts to the pupal stage with and without Tanglefoot did not differ significantly (for exposed [not sleeved]: t = 0.21, df = 6; P = 0.84; for sleeved: t = 2.43, df = 6; P = 0.051). Survival to the pupal stage in cohorts without organdy sleeves averaged 3.0 ± 2.9% with Tanglefoot and 3.7 ± 2.7% without Tanglefoot (pooled over all experimental runs). Survival to the pupal stage for cohorts on sleeved pots averaged 36.3 ± 6.6% with tanglefoot and 27.3 ± 3.4% without Tanglefoot (Table 1).

Because *C. rubecula* kills its hosts in the fourth instar, we also compared rates of survival to the fifth instar for treatments in all 4 runs. Differences in the survival of experimental cohorts to the pupal stage with sleeves (presence vs. absence) and tangle foot (presence vs. absence) as factors were highly significant (F = 53.4; df = 3; P < 0.0001). Survival to the fifth instar in cohorts without organdy sleeves averaged 5.3 ± 2.9% with Tanglefoot and 5.0 ± 1.3% without Tanglefoot (pooled over all experimental runs). Survival to the fifth instar for cohorts on sleeved pots averaged 43.0 ± 8.7% with Tanglefoot and 33.4 ± 5.2% without Tanglefoot (Table 1).

The survival of larvae in cohorts (Fig. 2) in all treatments decreased at a steady rate after an initial sharp drop between the first and second instar (which was seasonally more obvious in July and August), which was likely due to a combination of predation and failure of young larvae to establish and feed. There was another sharp drop in the number of larvae (considering visually parasitized larvae as "dead" for this comparison) in the unsleeved treatments during the fourth instar,
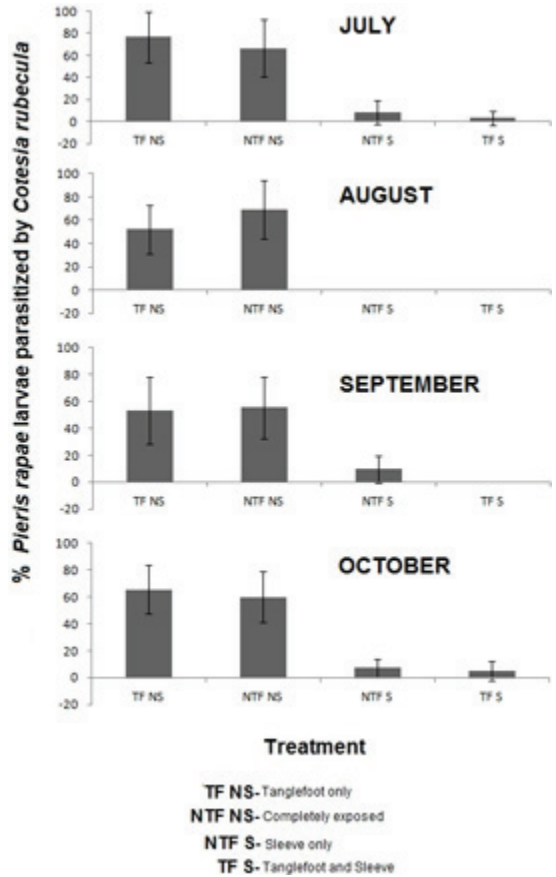

Fig. 2. The number of surviving *P. rapae* larvae (from first instar to pupa) in artificial cohorts established on potted collards in 4 successive months in 2011 on an organic vegetable farm in Westhampton, Massachusetts, USA. All cohorts began with 75 larvae on day zero. "Healthy" is defined as larvae that are alive, present, and not visibly parasitized (early stage parasitism is not detectable in living larvae). Numbers in parentheses on the x-axes are the dominant instar in the cohort on that sample date.

due to the effect of parasitism by *C. rubecula*. The fourth instar was the first point at which parasitism could be scored visually and was the instar in which larvae parasitized by *C. rubecula* died.

Parasitism of *P. rapae* by *C. rubecula*

Comparison of visually determined rates of parasitism to rates seen in larval dissection for 48 fourth instars placed in the experimental plot for this purpose (on the same dates as the cohort larvae in the main experiment) revealed that our estimates of the rates of parasitism by visual determination was 94% accurate. For these larvae, rates of parasitism based on visual inspection (65%) versus dissection of the same larvae (71%) were not sig-

nificantly different based on an unpaired t-test (t = 0.81; df = 4; P = 0.47). The few cases of error in assessing parasitism visually were larvae that appeared unparasitized in the field but found to be parasitized upon dissection. There were no cases of larvae being classified as parasitized in the field by visual inspection that upon dissection were found not to be parasitized. Consequently, our reported parasitism rates are conservative.

A 2-factor (month, treatment) factorial ANOVA found that there was no effect of month on parasitism rates (F = 0.0805; df = 3; P = 0.97), and therefore data on parasitism were pooled by month to examine the effects of treatments on rates of parasitism. For treatments lacking organdy sleeves the rate of parasitism by *C. rubecula* was high (62.4 ± 8.6 %) (Fig. 3), in contrast to treatments protected by organdy sleeves, in

which very little parasitism occurred (4.2 ± 4.0%) (ANOVA: F = 66.73; df = 3; P < 0.001). As with the survival data, the only significant difference in parasitism rates was between sleeved and exposed plants, with no effect of the presence or absence of tanglefoot on pots (Table 1).

Cohort Life Tables and Marginal Rates of Parasitoid Attack

Life tables for all treatments (4) by all runs (4) were constructed (16 tables) and examined. However, since run date (month of experiment) had no significant effect on any survival or parasitism parameters examined, tables were collapsed across run dates within treatments and the resultant 4 summary life tables, one per treatment, are presented (Table 2).

In a 3-way ANOVA of the effect of treatment, instar (first through fourth only) and run date on survival, we found no significant 3-way interaction (F = 0.75; df = 27; P = 0.65), but there was a significant effect of run date on survival during the early instar stages in all treatment types (F = 2.8, df = 3, P = 0.045). For this analysis, parasitized fourth instars were considered alive. Specifically, there was a significant difference between survival of all instars (first through fourth only) in all treatment types between the July and October experimental runs, but not between survival of instars in all treatment types of any other months based on a Tukey HSD test.

Marginal rate analysis (Table 1) revealed that parasitoid attack rates summed over both unsleeved treatment types (with and without Tanglefoot) were on average 13 percentage points higher (59.5 vs. 72.5%) than the apparent parasitism by *C. rubecula* as directly observed in field sampling.
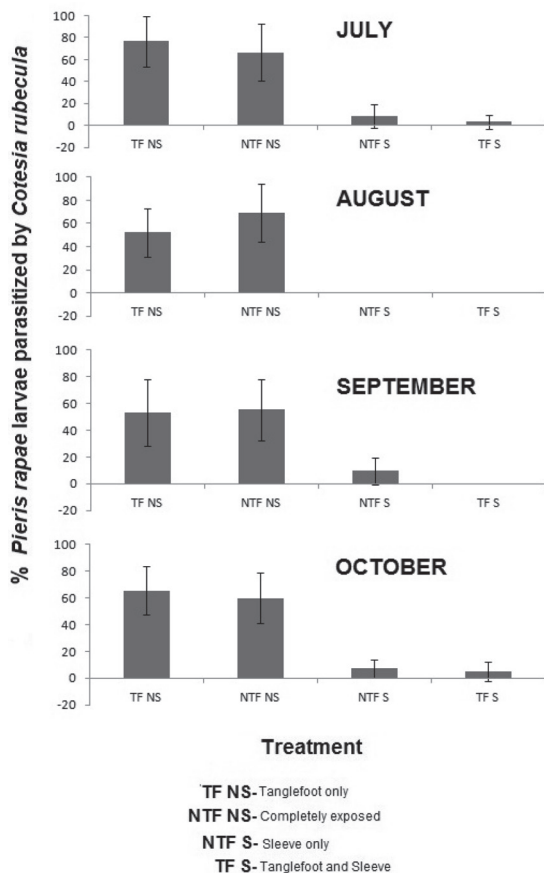

Fig. 3. Percentages of *Pieris rapae* larvae in experimental cohorts on potted collards that were parasitized by *Cotesia rubecula* during their larval life. Parasitism (± 95 % C.I.) is shown for 4 levels of natural enemy exclusion (with and without sleeve, and/or tanglefoot on pots), in 4 successive months in 2011 at an organic vegetable farm in Westhampton, Massachusetts.

DISCUSSION

Because it is often not feasible to monitor a biological control agent for many years after its release, an alternative is to measure the effects of the biological control agent after a lapse of some years, after it has had an opportunity to become fully effective. Monitoring cohorts of individuals with known and standardized age structures and starting points can provide especially useful data. In this case, use of cohorts of *P. rapae* larvae on potted collard plants placed on an organic farm, with and without natural enemy exclusion, allowed us to quantify losses by instar, giving a more precise measure of the survival patterns of *P. rapae* life stages in the field over time. Monitoring cohorts allowed us to determine that there is a relatively large drop in survival (72.5%) between the fourth and fifth instars due to parasitism by *C. rubecula* (see Table 2, average marginal rates

TABLE 2. LIFE TABLES FOR COHORTS OF *PIERIS RAPAE* LARVAE ON POTTED COLLARDS DEPLOYED IN A COLLARD PATCH AT AN ORGANIC VEGETABLE FARM, INTERVALE FARM, IN WESTHAMPTON, MA, SUMMED OVER 4 MONTHS (JUL, AUG, SEP, OCT) IN 2011, WITH 4 LEVELS OF NATURAL ENEMY EXCLUSION (+/-TANGLE FOOT ON POTS CROSSED WITH +/-SLEEVES OVER PLANTS).

Tangle foot No Sleeve

| | | Stage | | Factor | | Apparent mortality | |
| | | | | | Marginal attack rate | Stage | Factor |
Stage	Factor	lx	dx	dx		qx	qx
L1		300	147			49	
	Disappeared			147			49
L2		153	43			28	
	Disappeared			43			28
L3		110	37			34	
	Disappeared			37			34
L4		73	57			78	
	Disappeared			13			18
	Parasitized[1]			44	73		60
L5		16	7			44	
	Disappeared			7			44
P		9					
	Not observed						

No Tangle foot No Sleeve

| | | Stage | | Factor | | Apparent mortality | |
| | | | | | Marginal attack rate | Stage | Factor |
Stage	Factor	lx	Dx	dx		qx	qx
L1		300	144			48	
	Disappeared			144			48
L2		156	28			18	
	Disappeared			28			18
L3		128	62			48	
	Disappeared			62			48
L4		66	51			77	
	Disappeared			12			18
	Parasitized[1]			39	72		59
L5		15	4			27	
	Disappeared			4			27
P		11					
	Not observed						

[1]In all cases, parasitized *Pieris rapae* larvae were parasitized by *Cotesia rubecula*.

TABLE 2. (CONTINUED) LIFE TABLES FOR COHORTS OF *PIERIS RAPAE* LARVAE ON POTTED COLLARDS DEPLOYED IN A COLLARD PATCH AT AN ORGANIC VEGETABLE FARM, INTERVALE FARM, IN WESTHAMPTON, MA, SUMMED OVER 4 MONTHS (JUL, AUG, SEP, OCT) IN 2011, WITH 4 LEVELS OF NATURAL ENEMY EXCLUSION (+/-TANGLE FOOT ON POTS CROSSED WITH +/-SLEEVES OVER PLANTS).

No Tangle foot with Sleeve

| | | | | | | Apparent mortality | |
| | | Stage | | Factor | Marginal attack rate | Stage | Factor |
Stage	Factor	lx	dx	dx		qx	qx
L1		300	74			25	
	Disappeared			74			25
L2		226	36			16	
	Disappeared			36			16
L3		190	51			27	
	Disappeared			51			27
L4		139	37			27	
	Disappeared			31			23
	Parasitized[1]			6	5		4
L5		102	20			20	
	Disappeared			20			20
P		82					
	Not observed						

Tangle foot with Sleeve

| | | | | | | Apparent mortality | |
| | | Stage | | Factor | Marginal attack rate | Stage | Factor |
Stage	Factor	Lx	dx	dx		]qx	]qx
L1		300	64			21	
	Disappeared			64			21
L2		236	30			13	
	Disappeared			30			13
L3		206	47			23	
	Disappeared			47			23
L4		159	23			14	
	Disappeared			21			13
	Parasitized[1]			2	1		1
L5		136	27			20	
	Disappeared			27			20
P		109					
	Not observed						

[1]In all cases, parasitized *Pieris rapae* larvae were parasitized by *Cotesia rubecula*.

of attack of 4th instars by *C. rubecula* for two uncaged cohorts).

While tanglefoot had no or perhaps a marginally significant effect on survival of cohorts, sleeves were successful at reducing parasitism: survival of cohorts to pupae was much higher for cohorts with sleeves (31.8 ± 6.9%) than without (3.3 ± 2.7%). This suggests that parasitism rather than predation by ground predators was responsible for most *P. rapae* mortality in late instars (fourths), while, in contrast, predation by ground-dwelling predators was likely responsible for most *P. rapae* mortality in early instars (first through third), apart from failure of transplanted larvae to settle and feed. However, since this study was designed to estimate the effects of parasitism, our insights into predation are limited.

Our estimates of parasitism are likely to be underestimates for 2 reasons. First, parasitism in the field, measured visually, was determined to be only 94% accurate and was always in the direction of an underestimate. Secondly, parasitism rates in the cohort data were influenced by the problem of simultaneous mortality, since some larvae disappeared steadily in all exposed treatments, likely due to predation. As a correction for this issue, we calculated the underlying marginal rates of parasitism, which revealed underlying parasitoid attack rates that averaged 13 percentage points higher (59.5% vs 72.5%) than apparent mortality due to parasitism (Table 2) (Elkinton et al. 1992).

Our results are consistent with a study conducted in New Zealand that assessed the rates of parasitism of *P. rapae* by both *C. rubecula* and *C. glomerata* (Cameron & Walker 2002). It is clear that in western Massachusetts *C. rubecula* is now the dominant parasitoid of *P. rapae* and has displaced *C. glomerata,* as it did at many of the New Zealand sites studied by Cameron & Walker (2002) and in parts of North America (Biever 1992; Van Driesche 2008; Herlihy et al. 2012). In Massachusetts, *C. rubecula* attacked *P. rapae* at a higher rate in our 2011 cohort study than did *C. glomerata* in a previous study in 1985 and 1986 (Van Driesche 1988), in the same area before the introduction of *C. rubecula*. In general our results were similar to those found by Cameron & Walker (2002) in *P. rapae* populations with and without *C. rubecula*.

As expected, in comparison to the earlier study (Van Driesche 1988), the survival pattern of *P. rapae* has changed significantly since the introduction of *C. rubecula*. In the 1980s study, survival of *P. rapae* declined steadily throughout all life stages in the first generation each year. During the second, third, and fourth host generations, *C. glomerata* (the dominant parasitoid) caused approximately a 50% decrease in survival between the fifth instar and pupal stage. Since the displacement of *C. glomerata* by *C. rubecula*, the de-crease in survival of *P. rapae* is now both steeper (72.5%) and earlier, occurring between the fourth and fifth instars. This is an important result for organic vegetable growers because earlier mortality of *P. rapae* caterpillars reduces damage per larva.

Cotesia glomerata in western Massachusetts is now a less common species, but one that remains a component of the *P. rapae*/collards agroecosystem (Van Driesche 2008). Partial displacement of *C. glomerata* from *P. rapae* means its density on the landscape as a whole is also likely to be lower, which should help reduce its parasitism rates to native pierids such as *Pieris oleracea* Harris (Herlihy 2012).

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