Experimental Evaluation of Arthropod Predation on *Pieris rapae* (Lepidoptera: Pieridae) Eggs and Larvae in Cabbage

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ABSTRACT Knowledge of factors causing mortality in herbivorous insects is essential to developing a better understanding of their population dynamics and more effective strategies to manage their abundance in crops. In this study we used 2 methods of predator exclusion to evaluate the effects of arthropod predators on *Pieris rapae* L. eggs and larvae on cabbages (*Brassica oleracea* variety *capitata* L.) in New York State. Survivorship of *P. rapae* on cabbage plants caged to exclude predators was compared with survivorship on plants in cages that were opened at the bottom to allow access by arthropod predators but not larger predators such as birds. Two cohorts were followed in each of 2 unsprayed cabbage plots in each of 2 yr for a total of 8 cohorts. Estimated mortality of eggs and larvae from arthropod predators ranged from 23 to 80%, averaged 53% for all 8 cohorts, and affected mainly the eggs and 1st instars. Exclusion experiments were also conducted comparing mortality of individual *P. rapae* eggs protected from predators by rings of Tanglefoot with that of eggs that were left exposed to predators. Mortality attributed to arthropod predators for the entire egg stage among 6 cohorts placed in each of 2 fields ranged from 0 to 44%. Our experiments demonstrate that *P. rapae* eggs and 1st instars suffer variable, but often quite high mortality from arthropod predators in cabbage fields. Recognizing the important role of these predators is a 1st step toward developing ways to maximize their activity in commercial fields.

KEY WORDS *Pieris rapae*, predation, survival, mortality

NATURALLY OCCURRING ARTHROPOD predators significantly reduce pest populations in many crops (Hagen et al. 1976, Turnipseed and Kogan 1976, Ehler 1977, Jones 1982, Kenmore et al. 1984, Kröber and Carl 1991, Ruberson et al. 1994). Maximizing their contribution in pest management, however, often requires a recognition of their value and an understanding of factors affecting their activity (Gross 1987, Stinner and Bradley 1989, Dutcher 1993, Whitcomb 1994). This study represents a 1st step in our efforts to evaluate and enhance the role of indigenous arthropod predators in controlling the imported cabbageworm, *Pieris rapae* L., the most important foliar pest of crucifer vegetables in the northeastern United States and eastern Canada (Harcourt et al. 1955, Ferro 1993).

Arthropod predators are known to influence *P. rapae* populations in many parts of the world (Dempster 1967, Parker 1970, Ashby 1974, Hasui 1977, Jones et al. 1987), but their impact has not been evaluated in the important crucifer growing areas of the northeastern United States and eastern Canada. Life table studies have helped identify some of the agents causing mortality (e.g., parasitoids and pathogens) (Harcourt 1966, Van Driesche 1988). However, life tables are not as useful for evaluating effects of predators (Jones 1987). In most cases they fail to differentiate the action of predators from other agents, such as wind, rain, or host plant effects, that may cause insects to disappear between sampling times (Kyi et al. 1991).

Predator exclusion using field cages or other means is a common method for evaluating the impact of arthropod predators on pest populations (Luck et al. 1988, Kidd and Jervis 1996). In this study we compared survival of cohorts of *P. rapae* protected from arthropod predators with survival of cohorts exposed to predators in the field to determine if these predators significantly reduce *P. rapae* survivorship in cabbage (*Brassica oleracea* variety *capitata* L.). Two methods were used to exclude predators: cages around individual plants and sticky barriers around individual *P. rapae* eggs.

Materials and Methods

Predator Exclusion Using Cages. In 1995 and 1996, we compared survivorship of *P. rapae* on cabbage plants caged to exclude arthropod predators to that on plants in sham cages that allowed predator access. The experiments were conducted at the Fruit and Vegetable Crops Research Farm of the New York State Agricultural Experiment Station in Geneva, NY. Experimental plots each year consisted of two 0.2-ha square fields of 'Vantage Point' (1995) or 'Cheers' (1996) cabbage transplanted as seedlings on 2–5 July 1995 and 6–10 June 1996. Standard agronomic practices were used on the plots and no insecticides were applied. The 2 plots were separated by 590 m in 1995 and 160 m in 1996, and each was bordered by a 3- to 5-m strip in which weeds were controlled by disking

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and rototilling. In each plot, each year, survivorship of 2 cohorts was monitored, one after the other, during July, August, and early September, the months when *P. rapae* typically reaches economically damaging levels in this area (Shelton et al. 1983; A.M.S., unpublished data).

Vantage Point (1995, first 2 cohorts), 'Bravo' (1995, last 2 cohorts), or Cheers (1996) cabbage plants were grown in the greenhouse and exposed to ovipositing *P. rapae* from a laboratory culture until each plant had ≥5 eggs. The plants were then placed into the cabbage fields in cages designed to completely enclose the plants, both above and below ground. The cages consisted of a plastic pot (30.5 cm diameter) embedded in the soil so the lip of the pot was at the level of the soil surface. A no-see-um mesh bag (Balson-Hercules, Providence, RI) lined the bottom of the pot and was supported above the plant by a 2.5-cm mesh wire net cylinder (46 cm high) resting on the soil surface in the pot and held in place by 2 short bamboo stakes. The bags were tied at the top to exclude predators from the plants but allow access for sampling. A peat and vermiculite based potting mix was used in the pots. Sixty plants were placed into each field, replacing every 15th plant in every 3rd row and forming a grid (30.5 × 24.7 m) in the plot center. On each plant, a permanent marker was used to mark the locations of 5 well-spaced eggs on leaf undersides by marking the leaf's upper surface. Any additional eggs were removed. The density of 5 eggs per plant widely spaced on the leaf undersurfaces was intended to approximate typical *P. rapae* egg distributions. In the field, *P. rapae* is known to lay most of its eggs singly on leaf undersides (Richards 1940, Jones 1981, Stewart and Sears 1988). Densities of *P. rapae* eggs on cabbage vary greatly. Harcourt (1961), for example, recorded mean densities of 0.14–29.92 eggs per plant. The 5 eggs per plant density used in this experiment was high enough to allow detection of any treatment effects, yet low enough to ensure that no plants became severely defoliated during the experiment.

Plants at alternate points of the grid were designated as sham cage plants to allow entry by arthropod predators yet exclude larger predators and control for cage effects. The bottom 15 cm of the above ground portion of the mesh bags on these plants was cut away and the remaining upper portion fastened in place on the wire netting cylinder using straight pins. Field soil was then spread over the pot rims to form a continuous surface with the surrounding soil. At 2- to 6-d intervals, *P. rapae* eggs and larvae were counted and any newly oviposited eggs or colonizing aphids were removed from the plants. Sampling was terminated when most larvae had reached 5th instar, because *P. rapae* larvae often disperse before pupation (Richards 1940, Harcourt 1961). Younger larvae, however, do not normally disperse from suitable host plants (Harcourt 1961, Jones 1977), so dispersal from sham cage plants would not be the cause for any differences in density that arose during the experiments.

The July 1995 cohorts were set in place 3 d after oviposition and the 2 August 1995 cohort was placed in the field 1 d after oviposition. No eggs had hatched in either case. The remaining cohort in 1995 and all 4 cohorts in 1996 were placed in the fields the day of oviposition. For each cohort a 95% CI for total mortality caused by treatment effect (in this case exposure to arthropod predators) was constructed using Elston's method as described by Rosenheim and Hoy (1989). Survivorship curves for the 2 treatments were compared visually to determine stages at which most of the mortality occurred.

Predator Exclusion Using Sticky Barriers. During 1995, mortality of *P. rapae* eggs caused by arthropod predation was estimated by comparing survivorship of eggs exposed to predators to that of eggs protected from arthropod predators by sticky barriers. These experiments were conducted in the same plots and concurrently with the cage experiments. On each of 6 dates, from 10 July to 15 August, 6-mm disks bearing 1 *P. rapae* egg apiece were cut from parafilm oviposition sheets collected from a laboratory colony (Webb and Shelton 1988). The disks were pinned, 1 per plant, to the undersides of middle frame leaves of 100 plants in each field. The plants were chosen to form a grid (10 × 10) of ≈32 by 27 m in the center of the plots. Half the eggs in each plot (those on alternate points of the grid) were protected from arthropod predators by applying a ring of Tree Tanglefoot (Tanglefoot, Grand Rapids, MI) around the disk and egg using a syringe. Egg locations were marked on the upper leaf surface using a permanent marker. After 2 d, damaged, missing, and intact eggs were counted. Percentage of mortality resulting from arthropod predators was determined by using Abbott's (1925) formula to adjust the percentage of exposed eggs that were damaged or disappeared by the percentage of protected eggs damaged or disappeared. Occasionally a pin was found to have been dislodged from a plant, and those eggs were not included in the analysis.

Mortalities of protected and exposed eggs were compared for each plot using the likelihood ratio chi-square (G^2) test (PROC FREQ) (SAS Institute 1989). We then used our measurements of mortality over each 2-d period to estimate mortality that would occur had the eggs remained in the field from time of oviposition to time of hatch. Assuming predation rate, r, was constant throughout the egg stage, predation mortality over 2 d, M_2, equals 1 minus survivorship [$M_2 = 1 - \exp(-rt_2)$, where $t_2 = 2$ d]. The constant mortality rate can be calculated as $r = -\ln(1 - M_2)/t_2$, and this value can then be used to calculate an estimate for predation mortality expected over the duration of the egg stage, M_T, as $M_T = 1 - \exp[t_O \ln(1 - M_2)/t_2]$, where t_O equals duration of the egg stage. To account for the effect of temperature on development rate (and possibly predation rate), we calculated degree-days for each 2-d period that the eggs were placed in the fields. For development rate we used the mean of the development rates for eggs of 2 *P. rapae* populations studied by Jones and Ives (1979). Daily maximum and minimum temperatures were measured at a weather station located ≤775 m from the plots and used to calculate degree-days for each 2-d period (Allen 1976).

To get some indication whether or not mortality rates of the eggs on parafilm disks were similar to mortality of naturally deposited eggs, on 30 July the locations of 52 eggs were marked as they were laid by wild *P. rapae* flying in one of the plots. Tanglefoot was used to protect 22 of these eggs from arthropod predators, and damaged, missing, and intact eggs were counted 2 d later. Mortality caused by arthropod predators was then estimated as described above.

Results

Predator Exclusion Using Cages. *P. rapae* suffered greater mortality when exposed to arthropod predators than when protected from them, and most of the differences in survivorship between the 2 treatments arose during the egg or 1st instar (Fig. 1; Table 1). Estimated overall mortality caused by arthropod predators was often quite high but also quite variable, ranging from 23 to 80% (Table 1). Mean predation mortality across all 8 cohorts was 53%. The survivorship curves show that much of the mortality was common to both treatments, apparently arising from factors that acted equally on *P. rapae* in both cage types. The difference in the shape of the July 1995 curves (Fig. 1 A and B) and the others reflects the difference in stage distribution of the cohorts at the 1st sampling date. The July 1995 cohorts were placed in the fields shortly before hatch, so most individuals were 1st instars at the time of the 1st count, although in the other cohorts most were still eggs. Predators observed on the sham cage plants included syrphid, coccinellid, and chrysopid eggs and larvae; predaceous thrips; and spiders. The decrease in the final count for the August–September 1996 cohorts (Fig. 1 G and H) in the sham cages can be attributed to prepupation dispersal. The faster development in these cohorts resulted from warmer temperatures during this period.

Predator Exclusion Using Sticky Barriers. Over the 12 location/date combinations, a total of 588 protected and 595 exposed eggs was evaluated for evidence of predation. Such evidence included eggs partially or entirely consumed or eggs with their contents partially or wholly removed (i.e., by predators with sucking mouthparts). In total, 10.8 and 10.7% of the eggs exposed to arthropod predators were damaged or missing in fields A and B, respectively, compared with 0.7 and 3.8% of the eggs protected by sticky barriers. These differences were highly significant (field A $G^2 = 33.32$, df = 1, $P = 0.001$, $n = 592$; field B $G^2 = 11.13$, df = 1, $P = 0.001$, $n = 591$). After adjusting for the protected eggs that were missing or damaged, mortality of exposed eggs caused by arthropod predators was estimated at 10.2% in field A and 7.3% in field B. None of the protected eggs in the natural oviposition experiment were missing or damaged; therefore, in this case, estimated mortality caused by arthropod predators was equal to the percentage of damaged or missing of the exposed eggs, or 10.0%, which was close to the estimate of 12.2% for the eggs on disks placed in the same plot 1 d later (Fig. 2A, 1 August).

The eggs in our study were exposed for only a portion of the time normally spent in the egg stage. Calculated estimates of stage-long mortality for each period in each field are shown in Fig. 2 along with the 2-d mortalities adjusted for control mortality.

Placement of eggs on 9–11 August 1995 coincided with occurrence of the egg stage at the beginning of the 2nd cage exclusion experiment in field B (Fig. 2B). Because no eggs had hatched in the cage exclusion experiment by the time of the 11 August count, an independent estimate of egg predation could be calculated from the exclusion experiment data. The estimate for egg predation from the exclusion cage experiment, after adjusting for control mortality and proportion of the egg stage completed in the 3 d, was 3.2%, somewhat lower than the estimate of 8.8% from the eggs on disks.

Discussion

Although the 8 predation estimates from the exclusion cage experiments have wide confidence intervals (Table 1), together they provide convincing evidence of a high level of mortality resulting from arthropod predators in our plots. Alternative explanations cannot account for the large effects seen. Because *P. rapae* larvae are known to rarely leave a suitable host (Harcourt 1961, Jones 1977), the treatment effects are not likely a result of dispersal from the sham cage plants. Although birds were occasionally seen in the plots, they were excluded from all the experimental plants by the wire netting and cloth covers. Parasitism also would not account for the treatment differences, because the parasitoids known to attack *P. rapae* in our area kill only 5th instars or pupae (Pimentel 1961a, b; A.M.S., unpublished data). The use of sham cages was intended to reduce differential effects of wind and rain on the *P. rapae* in the 2 treatments. Although there was evidence that some sham cage plants may have received more rain splash from the soil surface than the completely enclosed plants, this effect was inconsistent across plants and across sampling periods, and we consider it unlikely to be the cause of the consistently high differences in mortalities we observed.

Other workers have found a wide range of levels of survivorship in *P. rapae* on untreated plants. In most cases, however, the studies were not intended to measure predation impact directly, so the data do not permit a clear distinction between mortality resulting from predation and mortality from other factors such as weather and host plant quality (Harcourt 1966, Parker 1970, Jones et al. 1987, Van Driesche 1988). In all cases, mortality caused by combined categories of predation, weather, and unknown causes was highest in the earliest stages as in our study, whereas parasitism and disease affected primarily late instars and pupae. Dempster (1967) and Ashby (1974), using serological techniques, found arthropod predators responsible for large reductions in early instars. Ashby and Pottinger (1974) also used exclusion cage experiments to demonstrate the importance of arthropod predation on early instars, and Jones (1987) used sticky barriers to show that ants were responsible for high levels of mortality of *P. rapae* larvae in Australia. All studies to date that have explicitly evaluated arthropod predation and distinguished it from other mortality factors have found it

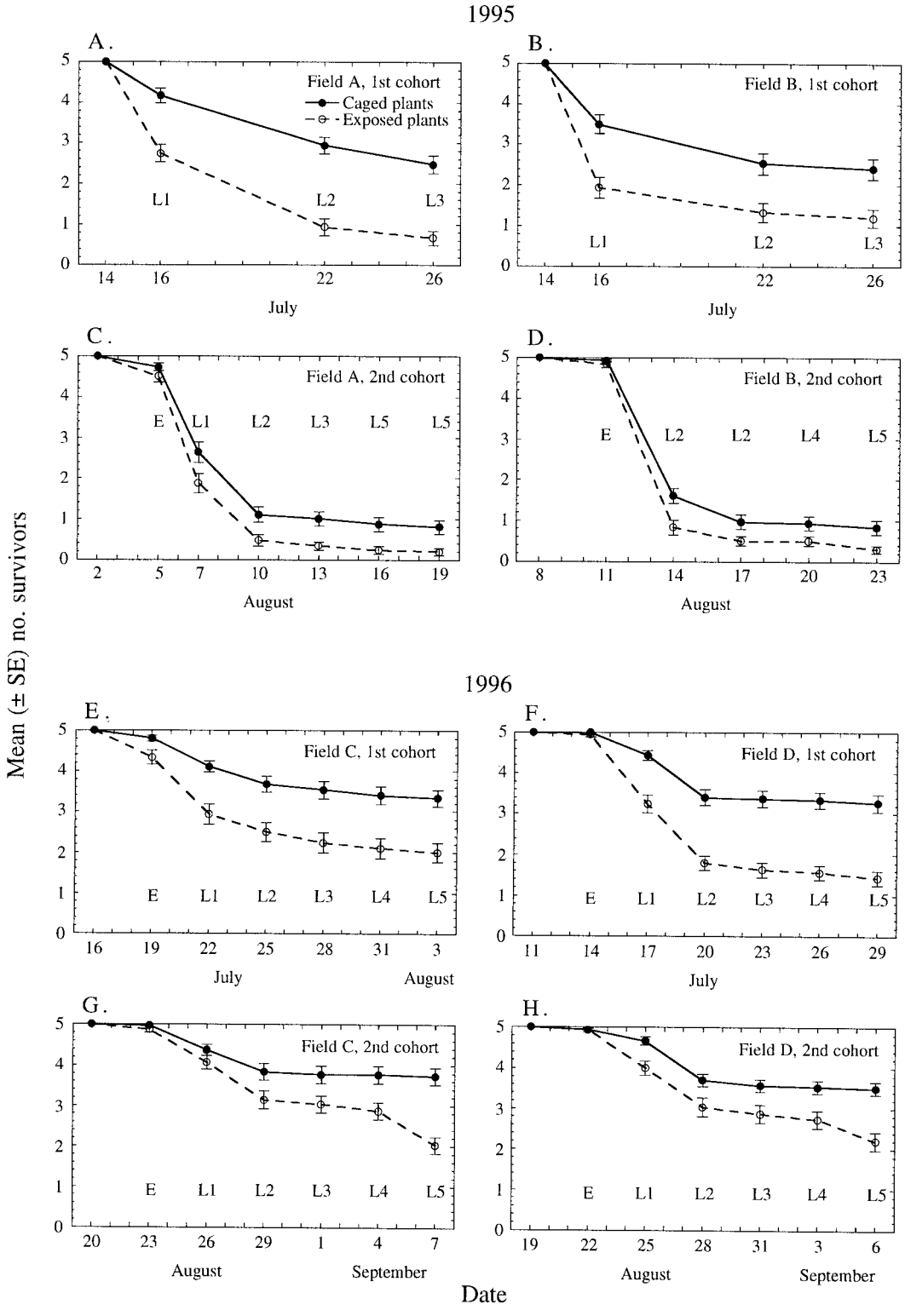

Fig. 1. Mean survivors from cohorts of 5 *P. rapae* eggs per plant protected from predators or exposed to arthropod predators. (A–D 1995, E–H 1996). In each treatment, $n = 30$ plants. E–L5 indicate stage containing the most individuals at each sampling date. Cohorts in bottom 2 plots (G and H) began dispersing for pupation before final count.

Table 1. Percentage of mortality of 8 cohorts of *P. rapae* eggs and larvae due to arthropod predation in cage exclusion experiments

Year	Field	Cohort	Mean (± 95% CI) % mortality of *P. rapae* eggs and larvae
1995	A	14–26 July	74 ± 15
		2–19 Aug.	80 ± 19
	B	14–26 July	52 ± 20
		8–23 Aug.	71 ± 20
1996	C	16 July–3 Aug.	41 ± 16
		20 Aug.–7 Sept.	25 ± 14[a]
	D	11–29 July	57 ± 12
		19 Aug.–6 Sept.	23 ± 14[b]

[a] Mortality calculated through 4 September, because prepupation dispersal had begun by time of final count on 7 September. On 4 September, most larvae had not reached 5th instar.

[b] Mortality calculated through 3 September, because prepupation dispersal had begun by time of final count on 6 September. On 3 September, most larvae had not reached 5th instar.

to be extremely important in reducing survival of *P. rapae* immatures. Our study demonstrated this effect experimentally in North America.

A number of life table studies have provided estimates for mortality of *P. rapae* eggs (Dempster 1967, Parker 1970, Ashby and Pottinger 1974). Life table studies, however, often overestimate egg mortality, because they cannot always distinguish mortality that occurred shortly after hatch (before the next sample is taken) from mortality occurring in the egg stage (Jones et al. 1987). Dempster (1967) recognized this difficulty and estimated egg mortality from his life tables by assuming a constant mortality rate and using data on mean egg survival time and mean time to hatch. For 3 generations on Brussels sprouts (*Brassica oleracea* variety *gemmifera* Zenk.) Dempster (1967) estimated dead and missing eggs as 5.8, 8.5, and 8.1%, similar to our more direct estimates.

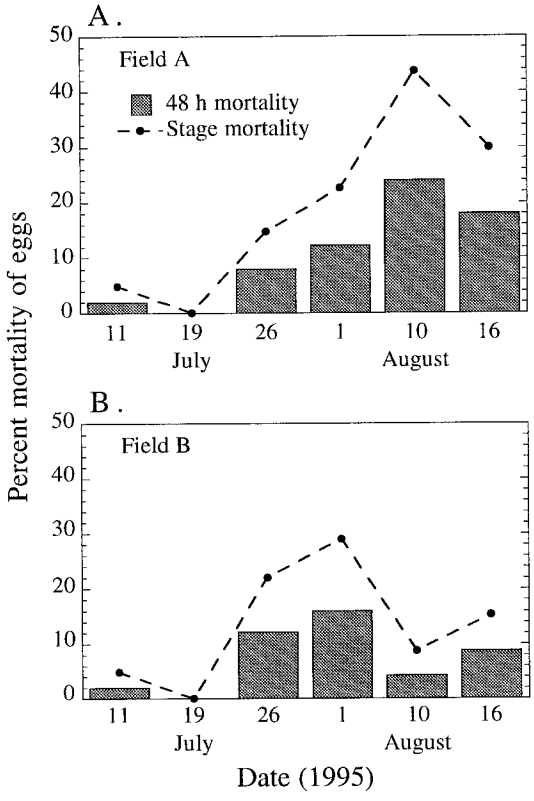

Fig. 2. Percentage of mortality of *P. rapae* eggs over 48 h from arthropod predation (adjusted for control mortality) and estimates of percent predation over entire egg stage in 2 cabbage plots (A and B) in 1995. Dates given are midpoint of each interval (e.g., for 11 July, eggs were placed on plants 10 July and examined 12 July). On 19 July, control mortality in both plots was slightly higher than that of exposed eggs.

Arthropod predation was significant in our exclusion cage experiments and was responsible for most of the mortality of eggs on parafilm disks. However, absolute mortality attributable to predators excluded by our cages was often less than that resulting from factors that were not excluded by the cages (Fig. 1). These factors could not be identified, but may include the effects of weather or host plant quality (Harcourt 1966, Hasui 1977, Jones 1981, Meyers 1985, Gilbert and Coaker 1988), or activity of very small predators such as thrips or mites that could penetrate the cage cloth. Pathogens could also be responsible, although we saw no evidence of disease during the experiments. Cannibalism of eggs by larvae has been observed (Jones 1981), but should not have been significant in our experiments because of the low densities and close age distribution of the cohorts.

As with all studies using exclusion techniques to estimate natural enemy impact, our results must be interpreted with caution. Although mortality of eggs on parafilm disks was similar to mortality of eggs deposited by wild butterflies, only a single small sample of the latter was taken, precluding a formal comparison of the two. Predation on artificially placed eggs or eggs and larvae in sham cages could differ from that on naturally occurring eggs and larvae for many reasons (Luck et al. 1988). Nevertheless, our experiments show that arthropod predation can have a significant impact on *P. rapae* populations in cabbage fields in our area and demonstrate the need for further investigation to determine the species responsible and means to conserve and enhance their activity.

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