Seasonal Ecology and Geographical Distribution of *Anaphes listronoti* and *A. victus* (Hymenoptera: Mymaridae), Egg Parasitoids of the Carrot Weevil (Coleoptera: Curculionidae) in Central Ontario

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ABSTRACT Field surveys were conducted during 3 yr in the Holland Marsh and district marshes to evaluate egg parasitism of the carrot weevil, *Listronotus oregonensis* (LeConte). *Anaphes listronoti* Huber was the dominant species in Ontario and was widely distributed in the sampled area. In commercial fields, up to 33% of the carrot weevil eggs were parasitized by *Anaphes* spp. In an untreated plot, parasitism averaged 68% and reached 94% in high density of carrot weevil eggs. Spring emergence of the parasitoids occurred from the end of April to mid-May, at which time the carrot weevil had begun its oviposition period in wild plants. Parasitoids had to complete between 1.6 and 2.3 generations outside the carrot fields before the appearance of carrot weevil eggs in plants. Parasitized eggs were observed in carrot fields from the beginning of the carrot weevil oviposition until September.

KEY WORDS *Anaphes listronoti, Anaphes victus, Listronotus oregonensis*, seasonal ecology, egg parasitoid

THE CARROT WEEVIL, *Listronotus oregonensis* (LeConte), is native to North America and is found in the northeastern United States and Canada (Perron 1971, Stevenson 1976, Simonet 1981, Collins and Grafius 1986b). It oviposits on umbelliferous plants and causes economic damage on carrots and occasionally on celery, particularly in the organic soils of the Holland Marsh area, Ontario (Stevenson 1976). Uncontrolled weevil populations may damage up to 40% of carrots (Boivin 1985). In Ontario, 2 foliar applications of insecticide against the adults, before females start to oviposit, provide effective control (Stevenson 1985), and an integrated pest management (IPM) program in the Holland Marsh area strives for reduction in the number of insecticide applications (Chaput 1993). This reduction could enable natural enemies to survive and allow effective control of carrot weevil populations.

Among the natural enemies of *L. oregonensis*, the braconids *Microbracon* sp. (Chittenden 1924) and *Aliolus curculionis* (Fitch) (Whitcomb 1965) have been mentioned as larval parasitoids. Two other species of parasitoids are known to attack carrot weevil eggs. One, *Anaphes listronoti* Huber, is found in Michigan, Ohio, and Quebec (Collins and Grafius 1986a, Boivin 1986), and a 2nd species, *A. victus* Huber, is present in Quebec and Michigan and is also found to parasitize the Texas carrot weevil, *L. texanus* (Stockton), in Texas (Boivin et al. 1990). Zhao et al. (1991) considered these egg parasitoids as the major biotic mortality factor for the carrot weevil in Quebec, and Collins and Grafius (1986a) reported that these parasitoids have little effect on this insect pest in Michigan. Two major differences may explain the controversy about the status of *Anaphes* spp. as a mortality factor of *L. oregonensis*. First, although the plot sampled has been insecticide-free for many years in Quebec, in Michigan sampling was done in a commercial field treated the previous year. These conditions favored higher carrot weevil density in Quebec and probably resulted in a higher level of parasitism by *Anaphes* spp. (Boivin 1993). Secondly, the egg parasitoids found in Quebec and Michigan were first identified as a single species, *Anaphes sordidatus* (Girault). They were recently reviewed and redescribed as 2 new species, *Anaphes listronoti* Huber and *Anaphes victus* Huber. The proportion of the 2 species was unknown in both Quebec and Michigan and therefore could have influenced the carrot weevil populations differently.

Little information is available on the seasonal activity of the egg parasitoids of *L. oregonensis* in

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an agroecosystem and their distribution in Ontario is unknown. The objectives of this research were to survey the egg parasitoids of the carrot weevil in the Holland Marsh and surrounding marshes in Ontario, and to report their seasonal ecology. Patterns of parasitoid and host occurrence and abundance were assessed in commercial carrot fields and in 1 insecticide-free carrot plot located on an experimental farm.

Materials and Methods

Carrot Plots. In 1990, sampling was done in Holland Marsh (44° 07′ N 79° 58′ W), Keswick Marsh (44° 18′ N 79° 50′ W), Cookstown Marsh (44° 20′ N 79° 63′ W), and Colbar Marsh (44° 13′ N 79° 55′ W), Ontario, in 11, 2, 1, and 1 commercial carrot fields, respectively, that were being monitored as parts of the IPM program operated by the Ontario Ministry of Agriculture, Food, and Rural Affairs (OMAFRA). In 1991 and 1992, we concentrated our work in the Holland Marsh and sampled 9 and 3 commercial fields, respectively. In each field, we delineated a plot (20 by 20 m) that was sampled from May to August. To avoid the negative impact of insecticides on *L. oregonensis* and its parasitoids, and to ensure availability of carrot weevil eggs to the parasitoids throughout the growing season, each year 3 plots were maintained as insecticide-free (hereafter referred to as untreated). The remaining plots received insecticide treatments as recommended by the IPM advisor. The cultivars, planting dates, fertilizer and pesticide treatments, and harvesting dates varied between fields. Commercial carrots fields were seeded generally by the beginning of May and carrot plants reached the 4th true-leaf stage in mid-June. Phosmet was the insecticide used against carrot weevil adults and diazinon, cypermethrin, permethrin, and carbaryl were applied to control carrot rust flies, *Psila rosae* (F.) (Diptera: Psilidae), aster leafhoppers, *Macrosteles fascifrons* (Stål), and cutworms (Lepidoptera: Noctuidae), as recommended by the OMAFRA (Chaput 1993). In addition, each year 1 plot (12 by 25 m) was located at the Muck Research Station (MRS) of OMAFRA in the Holland Marsh and was sampled from May (April in 1991) to September (October in 1990). This plot had not received any insecticide treatment for many years and it showed higher carrot weevil densities than in surrounding commercial fields. The preemergence herbicide prometryne was applied each year followed by hand-weeding in 1990 and 1991, whereas in 1992, weeds were controlled with linuron. Also in 1990, we sporadically sampled 1 carrot field located in mineral soil near Queensville (44° 12′ N 79° 39′ W) and 1 parsnip field in the Colbar Marsh. During the 3rd wk of May 1991, we sampled 5 commercials fields in Thedford-Grand Bend Marsh (43° 22′ N 81° 82′ W) and Komoka (42° 93′ N 81° 45′ W) areas.

Two techniques were used to determine which species of egg parasitoids attack the carrot weevil in Ontario and to evaluate their seasonal ecology.

Carrot Plants. To estimate the natural parasitism rates of carrot weevil eggs, 50 (1990–1991–1992) and 100 (1992 until July 21) carrot plants were sampled from the 2nd true-leaf stage until the end of August. A true-leaf stage was assigned when the leaves of a carrot plant were fully opened and at least 50% of the plants in the plot had the same growth stage. Every week from June to August, carrot plants were collected randomly from the plot, placed in plastic bags, and stored at 4°C until examination. Each stem was examined, and carrot weevil eggs were extracted, placed individually in polyethylene capsules (Boivin 1988b), and incubated at 24 ± 1°C and a photoperiod of 18:6 (L:D) h. The eggs were checked daily for emergence of adult parasitoids or carrot weevil larvae. After 21 d, unhatched eggs were dissected and classified as nonparasitized, parasitized, or unidentified cause of death. This last category included eggs damaged during manipulation, sterile eggs, and eggs killed by other causes, and it represented 13% of all eggs. Baudoin and Boivin (1985) estimated the percentage of sterile eggs laid by carrot weevil females at 8%, and our data suggested that ≈5% of mortality was the result of unidentified causes.

Carrot Baits. In each plot, carrot roots infested with carrot weevil eggs were placed as baits. Host eggs exposed in the plot were 1–4 d old, the age most accepted by *Anaphes* females (Picard et al. 1991). One sample consisted of 3 carrot baits containing carrot weevil eggs. The number of eggs in each carrot bait was not controlled and egg density varied from ≈25 to 200. To obtain these eggs, adult carrot weevils, obtained from the Horticultural Research and Development Centre (Agriculture and Agri-Food Canada at St-Jean-sur-Richelieu, PQ) were reared in a growth chamber according to the procedure described by Martel et al. (1975). Carrot baits, ≈3 cm diameter, were placed with ≈100 actively ovipositing carrot weevil females for 24 h, then checked for a minimum of 25 eggs, grouped in a plastic bag, and stored at 4°C for a maximum of 3 d. This temperature delays the development of carrot weevil eggs and does not affect the eventual rates of parasitism (G.B., unpublished data). The procedure was repeated until we obtained the desired number of carrot baits.

Weekly, throughout the sampling period, 3 carrot baits were deposited in each plot, at 5-m intervals and 5 m from the border. They were held to the ground by transpiercing them with a wire. Three days later they were removed, placed in plastic bags, and stored in the laboratory at 20–30°C until the eggs were extracted (within 24 h of collection). Twenty-five oviposition cavities were selected randomly in each carrot bait. In each cavity, we extracted the egg closest to the surface to avoid those unaccessible by the parasitoid ovipositor. Eggs were individually placed in polyethylene capsules, incubated, checked, and classified as described under carrot plants.

For both sampling techniques, percentage of parasitism was estimated from the number of eggs with parasitoid adults, either emerged or identified by dissection, on the total number of carrot weevil eggs minus those with an unidentified cause of death. Dates refer to the dates of removal of carrot baits and carrot plants.

Parasitoid Identification. *A. listronoti* and *A. victus* were recognized as distinct species only in 1992. Therefore, data from 1990 and 1991 refer to *Anaphes* spp. In 1992 the 2 species were identified based on biological characters. *A. listronoti* is a facultative gregarious parasitoid, whereas *A. victus* is strictly solitary at emergence (van Baaren et al. 1994, Nénon et al. 1995). Therefore, parasitoids that emerged 2 or more per carrot weevil egg were identified as *A. listronoti*. Solitary parasitoids were bred with the opposite sex of *A. victus* individuals of the Quebec population obtained from the Horticultural Research and Development Centre (Agriculture and Agri-Food Canada, Saint-Jean-sur-Richelieu, PQ). Laboratory tests occurred within 24 h of emergence, and individuals that successfully mated were recorded as *A. victus*. Unmated individuals were then bred with *A. listronoti* before being recorded.

Meteorological Data. Air temperature was recorded at ≈1.5 m above the ground and ≈3 m from the plot at the MRS. Degree-days base 7°C (Simonet and Davenport 1981) and 6°C (G.B., unpublished data), respectively, for the development of the carrot weevil and *Anaphes* spp., were calculated according to the method of Baskerville and Emin (1969).

Statistical Analysis. Improved angular [arcsine$\sqrt{(Y + 3/8)/(n + 3/4)}$] transformation and square-root transformation were performed, respectively, on the proportion of parasitized eggs and carrot weevil egg density to stabilize variance (Sokal and Rohlf 1981). Data were analyzed using general linear model (GLM) analysis of variance procedures and the Tukey studentized range test for means comparisons (SAS Institute 1982).

Results and Discussion

Species Richness. Two egg parasitoids of the carrot weevil, *A. listronoti* Huber, and *A. victus* Huber, were recovered from collections, respectively, in 20 and 2 carrot fields. The predominant species, *A. listronoti*, is gregarious and was encountered both in organic soil at Holland Marsh, Colbar Marsh, Keswick Marsh, Cookstown Marsh, and Thedford-Grand Bend Marsh and in mineral soil. The solitary parasitoid *A. victus* occurred sporadically in collections from the Holland Marsh and represented 10% of the parasitized eggs in 1992. Eggs parasitized by *A. victus* were found from 2 June to 8 September, but 95% of them were observed from July to September. In Texas, *A. victus* parasitizes 70.3 and 69.7% of its host eggs in carrot and parsley fields, respectively (Boivin et al. 1990). The low level of parasitism by *A. victus* in Ontario may be explained by a preference for alternative hosts. In contrast, the activity of *A. listronoti* was noted in most of the fields during the 3 yr of the study.

The evaluation of the number of parasitoid species attacking a given host is influenced by the sample size and ≈1,000 host individuals are needed to detect the maximum number of parasitoid species (Hawkins 1994). During the 3 yr of this study, 28,065 carrot weevil eggs were sampled from carrot plants and carrot baits. Only 456 eggs were laid by indigenous carrot weevil females in carrot plants. The remaining eggs were deposited on carrot baits by laboratory-reared carrot weevils. In the host-location process, adult parasitoids respond to stimuli arising from the host food plant, the host itself, or stimuli associated with the presence of the host (Vet and Dicke 1992). Eggs laid in carrot baits may provide a set of stimuli different from those associated with eggs laid in carrot plants. Therefore, they may misrepresent the species richness of the carrot weevil egg parasitoids in carrot plants.

Carrot Plants. Carrot weevil oviposition started in June–July in all plots, and eggs were found until August except in 1990 when no eggs were observed in August in commercial plots (Table 1). Each year, egg density was lower in commercial plots than at the MRS (1990: $F = 222.54$; df = 2, 116; $P < 0.0001$. 1991: $F = 41.26$; df = 2, 73; $P < 0.0001$. 1992: $F = 9.21$; df = 1, 26; $P = 0.0054$). Insecticide treatments are effective against weevil adults (Stevenson 1983) and they reduced the egg densities in commercial fields. However, differences in egg density was not detected in commercial fields between untreated and treated plots because of the high variability and the small sample size.

Anaphes victus was reared from 6% of the carrot weevil eggs extracted from carrot plants in 1992. Although we did not know the actual percentage of parasitism by *A. victus* in 1990 and 1991, data from 1992 suggests that few eggs were parasitized by this species. In 1990 and 1991, the mean number of parasitoids per carrot weevil egg averaged 2.23 ± 0.99 and, whereas solitary parasitoids emerged in 25% of the parasitized eggs in 1990 and 1991, a portion of these was parasitized by *A. listronoti* because this species is facultative gregarious. In 1992, 75% of the solitary parasitoids were *A. listronoti*. Therefore, *A. listronoti* parasitized most of the carrot weevil eggs deposited in carrot plants. In Michigan, although the 2 species were not recognized, *A. listronoti* seems to be the dominant species because a mean number of 2.23 parasitoids emerged per parasitized egg (Collins and Grafius 1986a). In Quebec, *A. listronoti* represents

Table 1. Parasitism of carrot weevil by *Anaphes* spp. in eggs extracted from carrot plants sampled in commercial fields and at the MRS during the summers of 1990–1992

Site	Sampling period	Period with eggs in plants	Period of parasitized eggs	No. eggs per 50 plants	Mean% parasitism	No. parasitoids per eggs
			1990			
MRS	8 June–20 Aug.	18 June–20 Aug.	18 June–20 Aug.	24.80 ± 12.04a	79.43 ± 9.31a	2.31 ± 0.99
Commercial untreated	4 June–13 Aug.	11 June–23 July	25 June–23 July	1.70 ± 2.29b	32.90 ± 40.33b	2.21 ± 0.70
Commercial treated	8 June–13 Aug.	25 June–23 July	25 June	0.10 ± 0.34b	12.50 ± 35.35b	1.00 ± 0.00
			1991			
MRS	10 June–19 Aug.	10 June–19 Aug.	10 June–19 July	8.36 ± 6.92a	23.31 ± 21.09a	1.80 ± 0.96
Commercial untreated	10 June–19 Aug.	10 June–12 Aug.	—	0.72 ± 1.07b	0.00 ± 0.00a	—
Commercial treated	7 June–12 Aug.	10 June–24 June	10 June	0.23 ± 0.89b	25.00 ± 50.00a	1.50 ± 0.71
			1992			
MRS	16 June–24 Aug.	7 July–11 Aug.	21 July–11 Aug.	3.50 ± 4.64a	42.79 ± 47.88a	1.82 ± 0.53
Commercial untreated	16 June–24 Aug.	16 June–11 Aug.	—	0.30 ± 0.88b	0.00 ± 0.00a	—
			Pooled data			
MRS				12.69 ± 12.37a	49.39 ± 35.96a	2.24 ± 1.00
Commercial untreated				0.95 ± 1.69b	16.45 ± 32.53b	2.21 ± 0.70
Commercial treated				0.15 ± 0.60b	16.67 ± 38.93ab	1.33 ± 0.58

Means within the same year followed by the same letter are not significantly different at $P > 0.05$ based on Tukey test.

>85% of the parasitized carrot weevil eggs (G.B., unpublished data). In all these studies, *A. victus* represented a low proportion of the parasitized eggs and therefore probably do not represent an important mortality factor for the carrot weevil eggs.

Parasitized eggs were found throughout the weevil oviposition period except in commercial plots where no parasitized eggs were found in 1992 (Table 1). In 1990, the percentage of parasitism was higher at the MRS than in commercial plots ($F = 11.00$; df = 2, 26; $P = 0.0003$) but no difference was observed in 1991 ($F = 2.39$; df = 2, 19; $P = 0.1189$) and in 1992 ($F = 2.24$; df = 1, 7; $P = 0.1785$). Pooled data for the 3 yr indicated that the percentage of parasitism by *Anaphes* spp. is higher at the MRS than in commercial plots ($F = 6.37$; df = 2, 57; $P = 0.0032$). No difference was observed in commercial fields between treated and untreated plots. Although egg density and parasitism decreased from year to year in commercial plots, only egg density decreased at the MRS.

At the MRS, no constant pattern of carrot weevil oviposition could be detected. In 1990, oviposition was high from mid-June to mid-August and peaked during July (Fig. 1). In 1991, egg density was lower and 93% of the oviposition occurred from mid-June to mid-July. In 1992, only 32 eggs were found, most of them in the 1st half of August. In 1990, a high level of parasitism was observed at the beginning of the carrot weevil oviposition and it remained high during all the growing season. The maximum rate of parasitism was 94% and the seasonal average was 79%. In 1991, 23% of carrot weevil eggs were parasitized, with a peak of 44%, and in 1992, 43% of the eggs were parasitized. Similar high levels of parasitism have been observed in Quebec for *Anaphes* spp. in a plot untreated for many years (Boivin 1986, 1993; Zhao et al. 1991). However, in a commercial field in Michigan, 22% of weevil eggs were parasitized (Collins and Grafius 1986a), a level similar to the level observed in our commercial plots. For *Anaphes* spp. the percentage of parasitism is dependent of the carrot egg density (Boivin 1993). Therefore, the high levels of parasitism observed at the MRS and in Quebec are probably caused by the high carrot weevil egg density in these plots, whereas the reverse is true for the low levels of parasitism observed in commercial plot in Ontario and Michigan.

A single carrot weevil larva makes a carrot root unmarketable (Whitcomb 1965) and despite high levels of parasitism, control will be effective only if all eggs in a carrot plant are parasitized. At the MRS, all eggs were parasitized in 78, 33, and 53% of infested carrot plants, respectively, in 1990, 1991, and 1992 (Fig. 2). However, almost every week during the 3 yr, a proportion of the carrots had unparasitized eggs, but this proportion never exceeded 12%. This may indicate the presence of a refuge for the carrot weevil (dark gray area) in

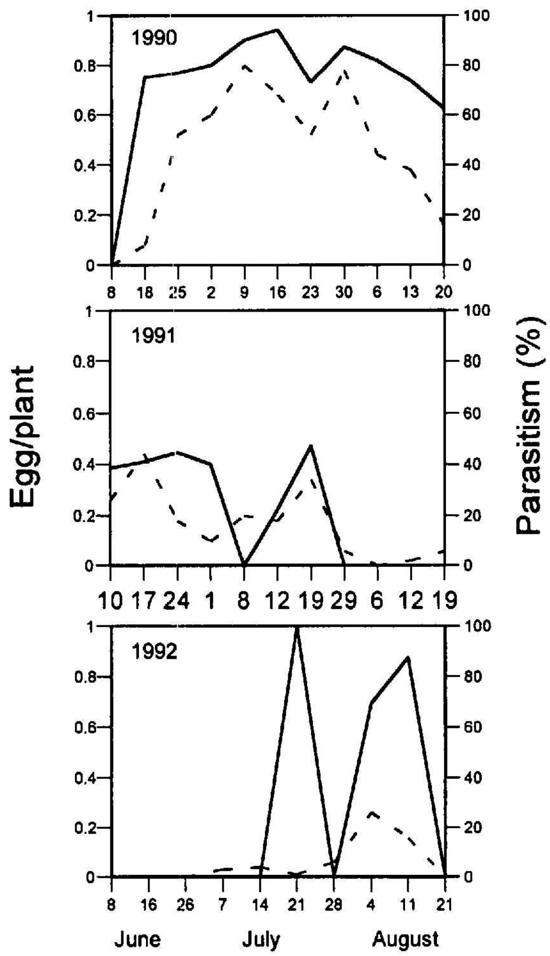

Fig. 1. Seasonal fluctuations of carrot weevil egg densities (broken line) and percentage of parasitism (solid line) by *Anaphes* spp. observed in the carrot plot of the MRS in 1990, 1991, and 1992.

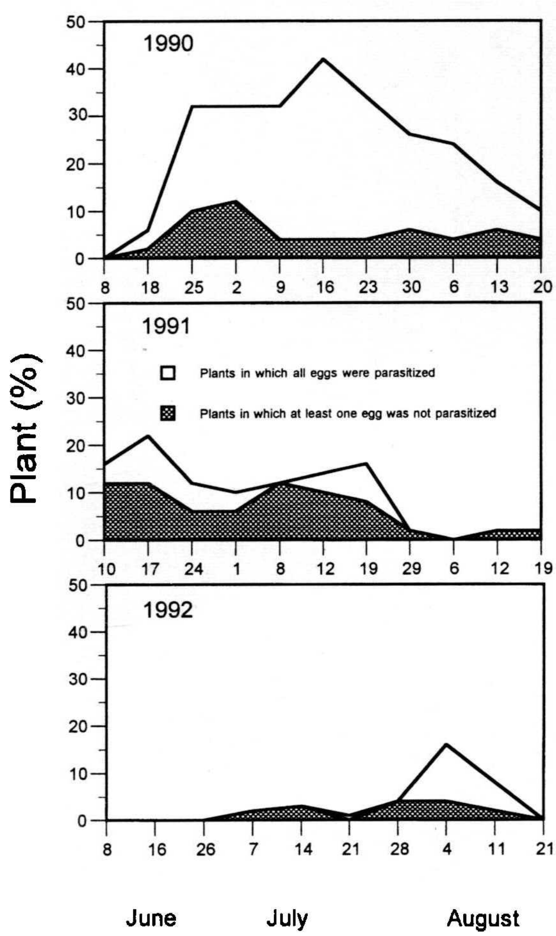

Fig. 2. Percentage of carrot plants with carrot weevil eggs at the MRS in 1990, 1991, and 1992.

which eggs did not suffer from attacks by *Anaphes* spp. Unparasitized eggs may result from the parasitoid behavior, the inaccessibility to microhabitat or lack of attractants to the host eggs (Crawley 1992).

Carrot Baits. Eggs in carrot baits were parasitized at every marsh, probably because of high host egg densities. At the MRS, the 1st parasitized eggs occurred early in the season each year. These eggs were parasitized by adults of the overwintering generation of *Anaphes* spp. because they occurred before 207 DD (base 6°C) (Table 2), the heat accumulation requirement for complete development (G.B., unpublished data). The spring emergence of *Anaphes* spp. was well synchronized with the beginning of oviposition by *L. oregonensis*. Based on the 1st appearance of parasitized eggs, the overwintering generation of *Anaphes* emerged from 105.5 DD (base 6°C), in late April or May (Table 2). *L. oregonensis* females are physiologically ready to oviposit in host plants from 147 DD (base 7°C) (Boivin 1988a), corresponding to 5, 12, and 21 May in 1990, 1991, and 1992, respectively. A maximum of 79.5 DD separated the emergence of overwintering parasitoids and the beginning of *L. oregonensis* oviposition, which is less than the degree-days accumulated during the longevity of

Table 2. Dates and cumulative degree-days base 6°C (in parenthesis) of the 1st parasitized egg and the beginning of carrot weevil oviposition in the carrot plot located at the MRS in 1990, 1991, and 1992

Event	1990	1991	1992
First parasitized egg extracted from carrot baits	9 May (199.25)	29 April (105.50)	15 May (129.75)
Carrot weevil females physiologically ready to oviposit (converted in base 6°C)	5 May (173.00)	12 May (179.50)	21 May (185.00)
First carrot weevil egg laid in carrot plants	11 June (443.50)	10 June (575.25)	23 June (464.00)

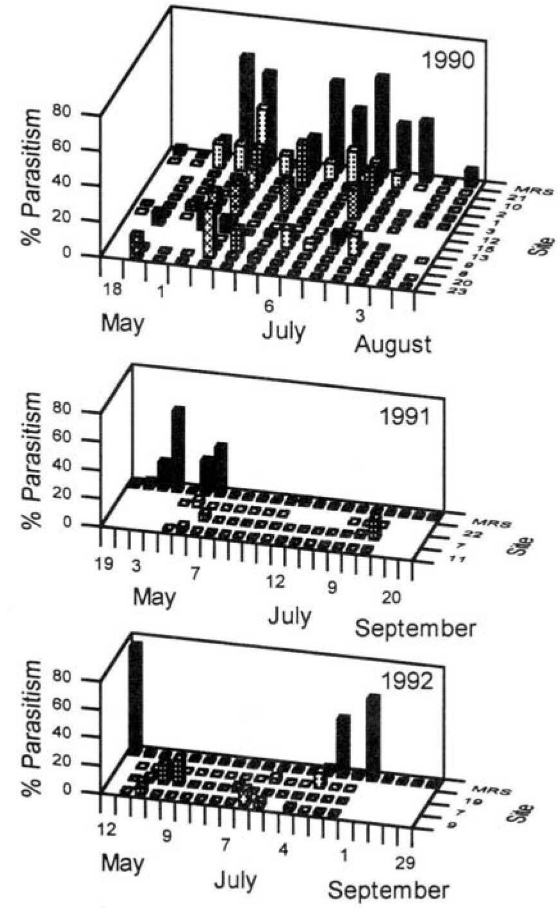

Fig. 3. Parasitism of carrot weevil by *Anaphes* spp. in eggs extracted from carrot baits deposited in commercial fields and at the MRS in 1990, 1991, and 1992.

Anaphes spp. adults (Collins and Grafius 1986b). However, in commercial fields, the carrots reached an acceptable developmental stage for carrot weevil oviposition only in June (Boivin 1988a) and therefore later than the emergence of the 1st *Anaphes* individuals. Carrot weevil eggs were thus found in the carrot field 5–6 wk after the emergence of the overwintering populations of *Anaphes* (Table 2). During this period, at least 338 DD had accumulated which is more than the longevity of *A. victus* and *A. listronoti* adults (Collins and Grafius 1986b). Therefore, *Anaphes* had to complete between 1.6 and 2.3 generations outside the carrot fields, either on *L. oregonensis* eggs laid on wild plants or on another weevil eggs, and then migrate to the carrot agroecosystem when carrot weevil eggs started to be laid.

The level of parasitism in carrot baits varied during the 3 yr and with location (Fig. 3). In 1990, 44% of the sites had a seasonal average of parasitism >3%, whereas in 1991 and 1992, only 1 plot had a mean percentage of parasitism above this value. The highest seasonal average of natural parasitism in the carrot plants was also observed in 1990, but the rates of parasitism observed in carrot baits were much lower (Fig. 3; Table 1). At least 2 reasons may explain this difference. Eggs are generally laid by *L. oregonensis* females in leaf petioles or crown of the plants and only 1% are observed in carrot roots (Boivin 1988a). Therefore, eggs in carrot baits are not in a natural microhabitat for *Anaphes* spp. and the parasitoids may not search for this unusual habitat. Second, eggs in carrot baits were exposed to parasitoid adults during a maximum of 3 d, whereas eggs in carrot plants could be exposed for longer periods because the plants were sampled weekly. Because *Anaphes* spp. are known to parasitize carrot weevil eggs up to 6 d old (Picard et al. 1991), the longer period of exposure would increase the likelihood of parasitism. Therefore, the observations derived from this technique is appropriate for indicating the presence of the *Anaphes* spp. and the timing of parasitism, but not for estimating the percentage of parasitism.

The 2 egg parasitoids of *L. oregonensis* parasitized 59% of carrot weevil eggs found in carrot plants. Highest parasitism occurred mainly in a noninsecticide treated plot having high carrot weevil egg density. Although parasitized eggs were found in 80% of the commercial fields, parasitism averaged only 17% in these fields. To increase the efficacy of both parasitoid species in field situation, further research is necessary to determine their respective spring hosts, their efficacy to locate and parasitize host eggs and their interactions in carrot fields.

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