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THE BIOLOGY OF PATASSON SP. NEAR SORDIDATUS (HYMENOPTERA: MYMARIDAE) AND ITS IMPACT ON THE CARROT WEEVIL

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THE BIOLOGY OF *PATASSON* SP. NEAR *SORDIDATUS* (HYMENOPTERA: MYMARIDAE) AND ITS IMPACT ON THE CARROT WEEVIL

by

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ABSTRACT

THE BIOLOGY OF PATASSON SP. NEAR SORDIDATUS (HYMENOPTERA: MYMARIDAE) AND ITS IMPACT ON THE CARROT WEEVIL

by

Robert D. Collins

Laboratory and field studies were conducted to examine the biology of Patasson sp. near sordidatus, a mymarid egg parasitoid of the carrot weevil, Listronotus oregonensis (LeConte), and to evaluate the impact of the parasitoid on host populations. Patasson sp. near sordidatus adults were short-lived, and both longevity and developmental times were influenced by temperature and superparasitism. Emergence periodicity was affected by both temperature and photoperiod. Courtship and mating behaviors were described.

Carrot weevil and parasitoid populations were spatially but not entirely temporally synchronous. Nominal parasitism rates (the overall percent of eggs parasitized) were found to overstate the true effect of the parasitoid on the weevil population due to the observed density-dependent weevil mortality in the absence of parasitism. The parasitoid was found to have a significant though minor role in carrot weevil mortality rates in the crop site.

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I. Introduction

The carrot weevil, Listronotus oregonensis (LeConte) was first reported as a pest of economically important crops in 1902 (Chittenden 1909). Its presence in Michigan was reported as early as 1915 (Henderson 1940), and it has since been observed to be widely distributed at low population densities in many vegetable growing areas within the state (Otto 1978). The primary crops attacked are parsley, carrots and celery, the latter two being of particular importance in Michigan. In Michigan, the carrot weevil is a periodic pest. Reports of damage have been sporadic, and economically significant infestation levels have generally been localized. However, severe damage in specific fields has occurred.

Prevention of economic damage by carrot weevils is primarily accomplished by crop rotation. Dispersal of this insect occurs as a result of walking. Flight appears to play no significant role in inter-field movement. This facilitates control by crop rotation and usually results in a confinement of infestations to field margins which are adjacent to fields infested during the previous growing season. Control of carrot weevil populations by the use of chemical insecticides is limited. There are no compounds currently registered in Michigan specifically for the control of the carrot weevil in crops other than celery. In addition, the incidental effectiveness of insecticides used for the control of other pest species is questionable. The egg and larval stages of the carrot weevil are spent in a relatively protected environment inside the host plant, and pupation occurs below the soil surface. Therefore, only adult weevils experience direct contact with insecticides applied as foliar sprays, and the effectiveness of these chemicals appears to be limited.

Significant effects of natural enemies on carrot weevil populations have not been reported. Several associations between carrot weevils and parasitoids or parasites have been observed (Chittenden 1924, Whitcomb 1965, Ryser 1975), but in each instance only a negligible impact on the weevil population was noted. However, a mymarid egg parasitoid was discovered attacking carrot weevil eggs in significant numbers during the 1979 growing season in Clinton County, Michigan. This parasitoid has been identified as Patasson sp. near sordidatus (E. Grissell, USDA Systematic Entomology Laboratory, personal communication), and appears to represent a new species. It will be referred to hereafter as Patasson n. sp. A survey conducted in 1980 revealed the presence of this parasitoid at several other locations in Michigan, including vegetable growing areas near Hudsonville and Grant (Ottawa and Newaygo Counties, respectively). Simonet (Ohio Agricultural Research and Development Center, personal communication) has since observed the presence of this parasitoid at Willard, Ohio (Huron Co.). This parasitoid may represent a significant factor affecting carrot weevil populations in Michigan and could contribute to the periodic and localized nature of weevil infestations.

In 1979, a series of studies was initiated to examine the biology of Patasson n. sp., and to evaluate the impact of this parasitoid on carrot weevil populations. The objectives of laboratory studies of the biology and life cycle of Patasson n. sp. were to: 1) examine the effects of temperature, sex, and the number of parasitoids developing per host egg on adult longevity; 2) determine the relationship between adult size and the number developing per host egg; 3) examine parasitoid fecundity as influenced by the number developing per host egg and mating status; 4) determine the temporal pattern of oviposition; 5)

estimate developmental rates and the effect of number per host egg, temperature, and sex; 6) estimate the sex ratio by examining adults reared from field-collected host eggs; 7) investigate the effect of temperature and photoperiod on the periodicity of emergence by adults from host eggs and the role of endogenous and exogenous mechanisms; and 8) observe courtship and mating behavior. These studies were designed to provide basic information concerning the biology of the parasitoid in order to more completely evaluate its role as an agent of biological control in field situations.

Additional laboratory and field studies were undertaken to investigate relationships between the carrot weevil and Patasson n. sp. The objectives of these studies were to determine the degree of spatial and temporal synchrony between host and parasitoid populations, to examine resource exploitation strategies by both the carrot weevil and by Patasson n. sp., and to evaluate the significance of interactions between the two sets of strategies. Carrot weevil oviposition strategies will determine the array of resources (host eggs) available to the parasitoid, and the way in which the parasitoid exploits the available host eggs will influence the efficiency with which the weevil utilizes its resources. A final study was conducted to evaluate the relative impact of chemical insecticide applications on host and parasitoid populations.

Relevant literature is briefly summarized in the appropriate sections of the following report. A more complete review of the literature concerning the carrot weevil, the genus Patasson, and the closely related mymarid genus Anaphes, is given by Collins and Grafius (1982).

2. Adult Longevity

The adults of species closely related to Patasson n. sp. are short lived. Estimates of mean adult longevity under a variety of conditions have ranged from less than two days for Anaphes flavipes (Anderson and Paschke 1970a) to 12 days for an unidentified Patasson species (Fisher et al. 1961).

Longevity has been found to be strongly influenced by temperature (Anderson and Paschke 1970a, Stoner and Surber 1971). Differences based on the sex of the individual have also been reported (Aeschlimann 1977, Ahmad 1979). The influence of superparasitism on developmental times and on the size of adults has been discussed (Anderson and Paschke 1969). However, the effect of superparasitism on adult longevity as a measure of overall vigor has not been examined.

Turnbull and Chant (1961) suggested that the availability of food for adult parasitoids may play an important role in their success as biological control agents. Several investigators have used various dilutions of honey in distilled water as a source of food for laboratory colonies of mymarid parasitoids (Balduf 1928, Kevan 1946, Ahmad 1979, Vidano et al. 1979). This was presumably done to increase the longevity and general vigor of the adults. However, no quantitative information is available concerning the effect of adult feeding on aspects of the life cycle.

The objective of this study was to examine the effect of various factors on the adult longevity of Patasson n. sp. The effects of temperature, sex, superparasitism and adult feeding were investigated. The relationship between superparasitism and adult size was also studied. This information will facilitate an understanding of parasitoid-host interactions in the field.

2.1 Methods

Carrot plants were collected from the border rows of an untreated area of field #3 at the Hammond farm near East Lansing, Michigan, during July, 1980. Carrot weevil eggs were extracted from the plants and placed individually in inverted 65 ml clear plastic containers on a 5.5 cm disc of Whatman #3 qualitative filter paper. Eggs were kept in an environmental chamber at 26° C with a light-dark cycle of 16:8 (photophase beginning at 0600 h). Distilled water was applied to the filter paper when necessary to maintain a high relative humidity. The eggs were monitored twice a day, at 0800 h and at 2000 h (± 1 h) and the emergence of adult parasitoids recorded.

2.1.1 Effect of Temperature

When the first parasitoid had emerged from the egg within a container, the container was randomly assigned to an environmental chamber set at 17, 20, 23, 26, or 29° C with a photoperiod of 16:8. The adults emerging from at least 50 parasitized carrot weevil eggs were monitored at each temperature. A larger number of host eggs were monitored at 26° C. Limitations on the number of available environmental chambers precluded the examination of all temperatures simultaneously.

Adult longevity was observed by monitoring the status of parasitoids within each container every 12 ± 1 h at 0700 h and 1900 h. The longevity of each parasitoid was estimated by assuming that both emergence and death occurred at the midpoints of the observed 12 ± 1 h intervals.

The parasitoids emerging from a single host egg were kept in the original rearing container throughout the period of observation to avoid potential injury

resulting from their transfer to individual containers. In some instances, individual parasitoids emerged from the same egg during different monitoring periods. When two or more adults of the same sex emerged from an egg during different periods and also died during different periods, the longevity of the specific individuals was ambiguous. This will not affect treatment means but will influence associated variances. The set of assumptions which yielded the greatest contribution to the treatment variance was selected in all such situations. The actual variance associated with any mean would thus be equal to or less than the reported value. These situations occurred infrequently and affected the variance estimates only slightly.

2.1.2 Adult Feeding

A honey and beer based diet (Table 1) was made available to the adult parasitoids at all temperatures. The diet was introduced onto the filter paper using a hypodermic syringe inserted through the soft plastic base of the container. Parasitoids were fed when the initial emergence was observed within each container and every morning thereafter as long as at least one adult remained alive. Approximately 0.05 ml of diet per container was used at each feeding.

To determine the effect of the artificial diet on adult longevity, a control group was given a diet of distilled water in the manner described above. The control group was maintained at 26° C with a photoperiod of 16:8.

2.1.3 Adult Size and Superparasitism

Between one and six parasitoids were observed to emerge from a single

Table 1. Composition of diet fed to adult Patasson n. sp.

Honey	200 ml
Old Milwaukee beer	300 ml
Ascorbic acid	10 g
L-cystene hydrachloride	2 g
Distilled water	500 ml

carrot weevil egg. The relationship between adult size and the number of parasitoids developing per host egg was examined. Several measures of body size were evaluated in a preliminary study, including thorax length, overall body length, antennal length, and head capsule width. Only head capsule width, which is unaffected by conditions encountered subsequent to emergence, was found to be consistently related to the number of parasitoids per egg. Head capsule widths were measured for parasitoids kept at 26° C subsequent to their death. Measurements were made with an ocular micrometer at 50 x. Each micrometer division was ca. 0.0092 mm.

2.2 Results

2.2.1 Superparasitism

Adult size (as measured by head capsule width) was inversely related to the number of parasitoids developing per host egg (Table 2). Females were slightly, but not significantly, larger than males within each parasitoid per host egg category (t-tests, $p>.05$).

The adult longevity of Patasson n. sp. was also found to be related to the degree of superparasitism. The longevity of all parasitoids (males and females) kept at 26° C decreased as the number of parasitoids developing in the host egg increased (Table 3). The most pronounced differences were observed between adults reared from eggs in which one, two, or three parasitoids emerged. This relationship is similar to that found between size and the degree of superparasitism. Therefore, longevity may be related to size. The correlation coefficient between mean adult longevity and mean head capsule width was 0.980 and is significant (t-test, $p<.01$).

Table 2. Mean head capsule width of adult Patasson n. sp. as affected by number of parasitoids per host egg and sex.

No. of parasitoids per egg	Mean head capsule width (mm)			
	Males	Females	Total[a]	
One				
Mean	Ø.244	Ø.256	Ø.252	a
SD	Ø.Ø18	Ø.Ø16	Ø.Ø18	
N	34	52	86	
Two				
Mean	Ø.212	Ø.22Ø	Ø.217	b
SD	Ø.Ø17	Ø.Ø17	Ø.Ø17	
N	63	1Ø3	166	
Three				
Mean	Ø.195	Ø.2ØØ	Ø.198	c
SD	Ø.Ø18	Ø.Ø19	Ø.Ø19	
N	51	84	134	
Four				
Mean	Ø.18Ø	Ø.185	Ø.182	d
SD	Ø.Ø25	Ø.Ø2Ø	Ø.Ø23	
N	18	15	33	
Five				
Mean	Ø.169	Ø.17Ø	Ø.169	e
SD	Ø.Ø12	Ø.Ø2Ø	Ø.Ø12	
N	8	2	1Ø	

a. Means followed by the same letter are not significantly different at p=Ø.Ø5, Student-Neuman-Kuel multiple range test.

Table 3. Mean longevity of adult Patasson n. sp. at 26 C as affected by sex and number of parasitoids per host egg.

No. of parasitoids per egg	Mean adult longevity (h)			
	Males	Females	Total[a]	
One				
Mean	100.42	83.17	90.00	a
SD	40.28	29.55	35.04	
N	38	58	96	
Two				
Mean	66.25	69.69	68.35	b
SD	27.06	25.11	25.80	
N	73	121	194	
Three				
Mean	59.24	60.68	60.14	c
SD	21.21	21.30	21.24	
N	63	105	168	
Four				
Mean	49.60	58.15	53.57	c
SD	23.94	22.44	23.16	
N	15	13	28	
Five				
Mean	52.80	---	52.80	c
SD	23.40	---	23.40	
N	5	---	5	

a. Means followed by the same letter are not significantly different at p=0.05, Student-Neuman-Kuel multiple range test.

2.2.2 Sex

The sex of the adult appears to have only a small effect on parasitoid longevity at 26° C (Table 3). A significant difference was found between the mean longevity of males and females only for adults emerging from host eggs in which they had developed singly (t-test, $p<.05$). For this group, the males lived an average of 20.7% (17.25 h) longer than the females. The females lived slightly (though not significantly) longer in all other categories. These data suggest that sex based differences in longevity play a relatively minor role in the dynamics of parasitoid populations in the field.

2.2.3 Survivorship

Survivorship of adult parasitoids kept at 26° C was relatively high during the first two days following emergence (Figure 1). After two days, 83.3% of all adults were still alive. Mortality increased over the next two days and only 17.7% were still alive after four days. A few adults remained alive up to 7.5 days after emergence.

Adult longevity has been shown to be related to the number of parasitoids developing per egg, and to a lesser degree to the sex of the individual. Thus, the survivorship curve of a particular field population would be determined in part by the distribution of individuals by parasitoid per egg category and by sex. The parasitoids examined in this study were reared from field collected eggs, and are thus assumed to be representative of the composition of the field population.

2.2.4 Adult Feeding

The average lifespan of adults reared from eggs in which one, two, three,

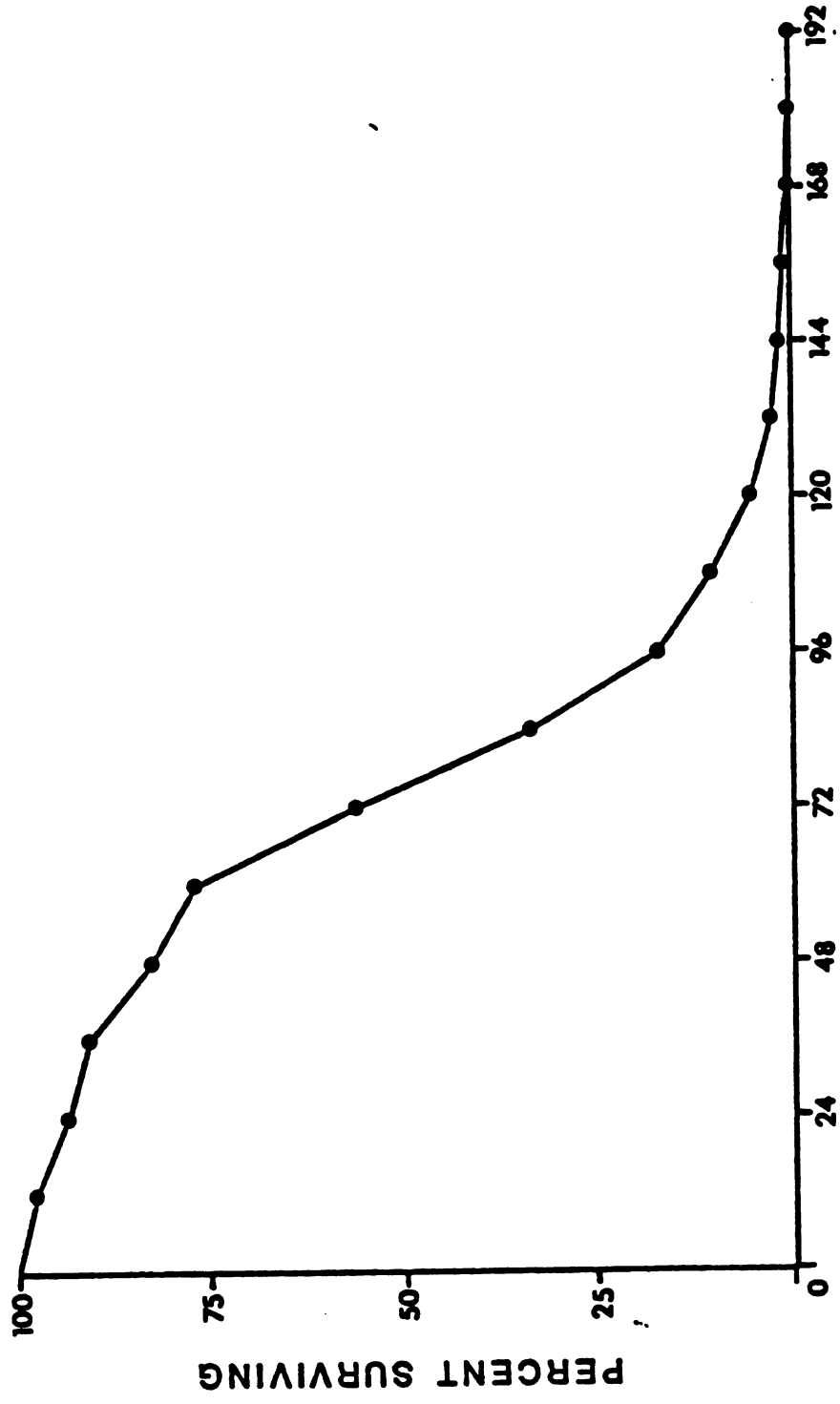

Figure 1. Survivorship of adult Patasson n. sp. at 26° C.

or four parasitoids developed increased 57.3, 74.4, 114.8, and 80.0% respectively when the honey and beer diet was made available (Table 4). Mean longevity was significantly greater in each parasitoid per egg category for parasitoids fed the artificial diet (SNK tests, $p<.05$). Insufficient data were available for comparisons involving adults from host eggs in which five parasitoids developed.

The relationship of feeding to other factors such as fecundity and the source of nutrition in the field is not known. However, feeding by the adults apparently plays an important role in the longevity of adults, and may consequently affect other aspects of the biology of this parasitoid.

2.2.5 Temperature

Significant differences have been demonstrated between parasitoid per host egg categories. Therefore, longevity comparisons between temperatures must be done independently for each parasitoid per egg category. These comparisons generally indicate an inverse relationship between temperature and longevity (Table 5).

Comparisons between the means for all adults at each temperature are not initially feasible because each temperature group consists of a different distribution among parasitoid per egg categories. However, overall comparisons can be made by weighting the mean longevity for each category by the fraction of parasitoids at all temperatures in the category. The means computed in this manner demonstrate the decreased longevity which occurred at increased temperatures for the parasitoids examined (Figure 2). Within the range of observed temperatures, longevity more than doubled as a result of a 10° C reduction in temperature.

Table 4. Effect of diet on mean longevity of adult Patasson n. sp. at 26 C.

No. of parasitoids per egg	Mean longevity (h) (males + females)[a]	
	Adults fed distilled water	Adults fed artificial honey diet
One		
Mean	57.20 a	90.00 b
SD	22.21	35.04
N	30	96
Two		
Mean	39.22 a	68.35 b
SD	14.74	25.80
N	56	194
Three		
Mean	28.00 a	60.14 b
SD	12.88	21.24
N	12	168
Four		
Mean	28.50 a	53.57 b
SD	10.99	23.16
N	8	28

a. In each row, means followed by the same letter are not significantly different at p=0.05, Student-Neuman-Kuel multiple range test.

Table 5. Mean longevity of adult Patasson n. sp. as affected by number of parasitoids per host egg and temperature.

Temperature	Mean adult longevity (h)[a]					
	Number of parasitoids per host egg					
	1	2	3	4	5	6
17 C						
Mean	230.00 a	165.60 a	128.67 a	109.28 a	122.40 a	---
SD	87.96	38.88	52.56	61.68	10.08	
N	12	30	45	28	5	---
20 C						
Mean	139.46 b	119.18 b	103.67 b	---	103.20 a	
SD	39.36	29.40	47.16	---	60.96	---
N	37	44	36	---	5	---
23 C						
Mean	156.00 b	94.87 c	74.00 c	72.37 b	44.00 b	54.00
SD	36.00	41.04	31.56	39.36	17.40	34.92
N	3	32	54	32	15	12
26 C						
Meam	90.00 c	68.35 d	60.14 d	53.57 bc	52.80 b	---
SD	35.04	25.80	21.24	23.16	23.40	---
N	96	194	168	28	5	---
29 C						
Mean	48.00 c	60.00 d	43.27 e	34.72 c	---	---
SD	---	17.76	22.08	22.68	---	---
N	1	40	66	28	---	---

a. In each column, means followed by the same letter are not significantly different at p=0.05, Student-Neuman-Kuel multiple range test.

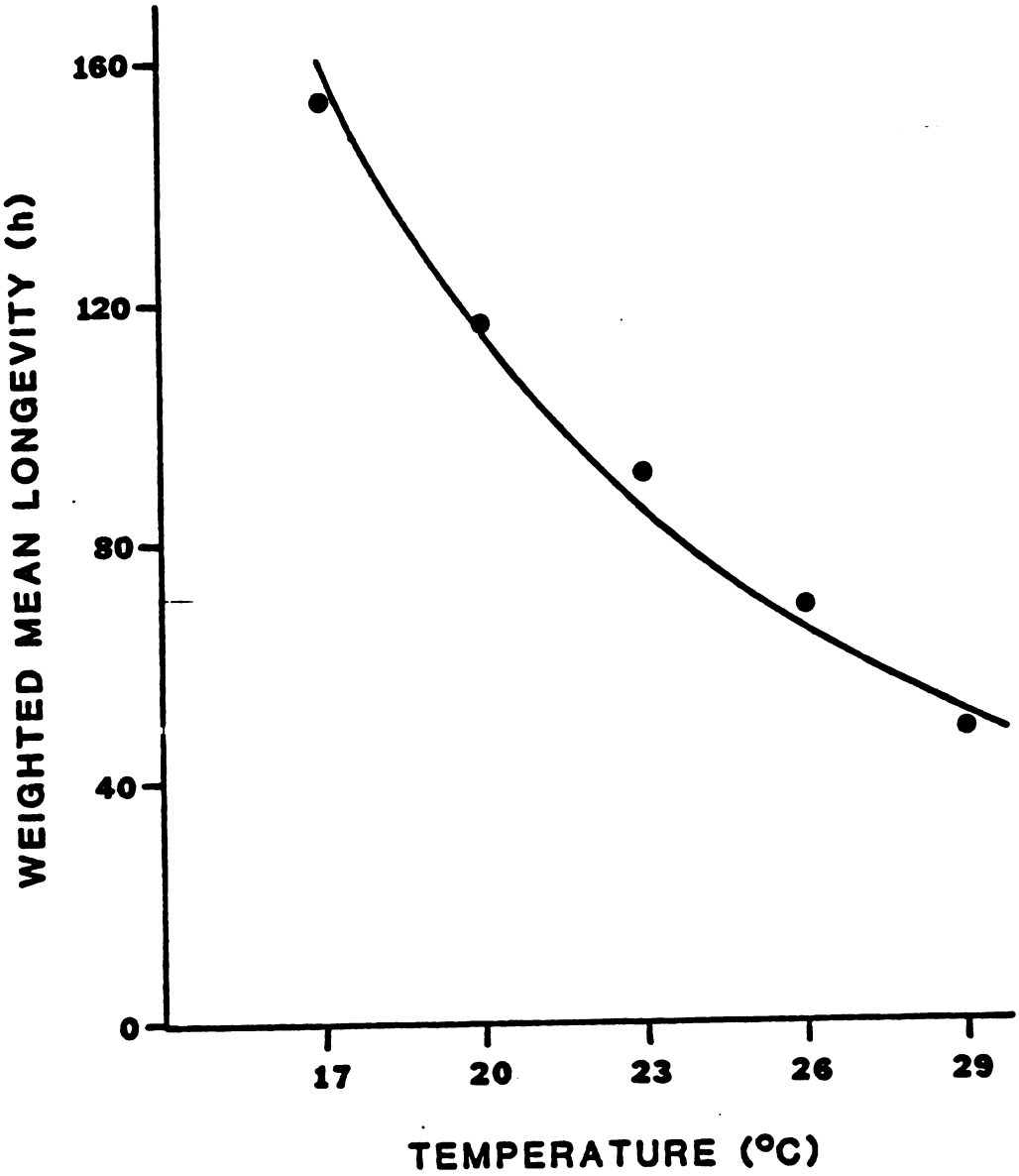

Figure 2. Effect of temperature on weighted mean longevity of adult Patasson n. sp. ($\log_e Y = 10.99 - 2.08 \log_e X$, $R = 0.981$).

2.3 Discussion

The results of this study show that Patasson n. sp. is relatively short lived. At 26° C, nearly two-thirds of the adults perished before reaching 3.5 days of age.

Adult feeding was found to influence adult longevity. The availability of an artificial diet increased mean longevity by more than 50% in all parasitoid per egg categories. In contrast, differences based on sex were relatively slight.

The degree of superparasitism appeared to have a major impact on adult longevity. Adults emerging from host eggs in which fewer parasitoids developed were larger and lived longer. This is apparently due to competition among the larvae for the fixed quantity of available resources. The greater the number of larvae within a host egg, the more intense is this competition.

The nature of the competition between parasitoid larvae within the host egg is not known. Interference competition may occur among some species. This is suggested for Anagrus atomus where only one adult successfully develops regardless of the initial number of parasitoid eggs within the host egg (MacGill 1934). However, mortality in most species does not increase appreciably until a high level of superparasitism is reached (Vidano et al. 1979, Statterthwait 1931, Anderson and Paschke 1969).

A typical result of lower levels of superparasitism is the production of smaller, less vigorous offspring (Jackson 1961, Chamberlin 1924, Anderson and Paschke 1969, Statterthwait 1931). The relationship between mortality prior to emergence as adults and superparasitism for Patasson n. sp. is not known. However, adults emerging from host eggs in which a larger number of parasitoids have developed were smaller and had a shorter lifespan. This suggests that

some form of exploitation competition may have occurred. In some species this competition may be reduced by the oviposition behavior of the female, which lays more eggs in larger host eggs than in smaller ones (Statterthwait 1931). However, this strategy may not be feasible when host eggs are scarce (Jackson 1961).

Temperature strongly influenced adult longevity. The relationships which were demonstrated may be useful in evaluating the effects of temperature variation on adult longevity in the field. However, estimates based on observations made under constant conditions may tend to overestimate the magnitude of such effects. In the field, the parasitoid may adjust the microenvironmental conditions in which it finds itself by changing locations, or by other adaptive behaviors. This will serve to dampen the amplitude of variations in macroenvironmental conditions and thus mitigate their effects on the parasitoid population.

3. Fecundity and Oviposition

Fecundity is generally low among Patasson and Anaphes species. Estimates of the mean number of progeny per female for various species have ranged from 17 to 36 (Williams et al. 1951, Anderson and Paschke 1970a, Stoner and Surber 1971, Aeschlimann 1977, Ahmad 1979). Oviposition usually begins soon after the emergence of the adult female (MacGill 1934, Williams et al. 1951, Jackson 1961, Anderson and Paschke 1969, Maltby et al. 1971). Most parasitoid oviposition occurs within the first few days in the life of the adult female (Kevan 1946, Williams et al. 1951).

Patasson and Anaphes are arrhenotokous; virgin females produce only male offspring by haploid parthenogenesis. Mated females produce progeny of both sexes. Anderson and Paschke (1968) stated that the female-male sex ratio among Patasson and Anaphes species is usually near 3:1. The sex ratio of field populations is dependent on both the percent of female offspring produced by mated females and the percent of virgin females.

Several aspects of Patasson n. sp. oviposition and fecundity were examined in this study. The effects of mating status and superparasitism were estimated. The sex ratio among the progeny of mated females was recorded, and the initiation of oviposition by newly emerged females was investigated.

3.1 Methods

3.1.1 Fecundity

Fecundity was examined by exposing carrot weevil eggs to adult female parasitoids and then rearing the eggs to determine the number of eggs parasitized and the number of progeny produced. Host eggs less than 24 h old

were obtained from a laboratory culture of carrot weevils known to be free of parasitism. The female parasitoids used in earlier trials were reared from host eggs collected from an untreated area of a carrot field at the Hammond Farm. Those used in later trials were obtained from weevil eggs which were parasitized in the laboratory. All of the females used in this study had emerged within six hours of trial initiation.

Each female parasitoid was kept in an inverted 65 ml clear plastic container with a moistened disc of filter paper. An artificial diet was introduced daily following the procedure described in Section 2.1.2. The females were kept in an environmental chamber at 23° C with a light-dark cycle of 16:8. Photophase initiation was at 0600 h.

Each trial involved the introduction of a group of carrot weevil eggs into a container with a female parasitoid. The eggs were introduced on a moistened wedge of cardboard with a central depression to prevent them from rolling off. Each host egg group was left in the container with the female for 24 ± 1 h, then removed and replaced by a new group of eggs. The host eggs were known to be 0-24 ± 1 h old at the time of their introduction, and 24-48 ± 2 h old at the time of their removal from the parasitoid container. A new group of eggs was presented to each female every 24 ± 1 h throughout her lifetime.

Female parasitoids were exposed to 20-50 host eggs during each 24 ± 1 h trial period. The number used was determined by the availability of host eggs and by parasitoid age. Preliminary results indicated that oviposition is relatively greater during the first few days following the emergence of the females from the host egg, and declines rapidly thereafter. Therefore, more eggs were used in trials involving younger females. Only three of 415 trials resulted in the

parasitization of more than 90% of the available eggs, and in no instance were all eggs parasitized. No individual female parasitized more than 39.7% of the eggs available to her during her life. It was thus assumed that host egg availability did not limit parasitoid oviposition.

The effect of mating status on fecundity was examined by recording the oviposition of females in three categories: 1) virgin females, 2) females allowed to mate once within two hours after their emergence and then denied further access to males, and 3) females kept in containers in which one or two males were introduced within two hours of female emergence and allowed to remain throughout the life of the female. Females in the third category were thus not precluded from mating more than once. The females used in all three categories emerged singly from their host eggs. This prevented mating except where desired.

The number of parasitoids which developed per host egg was shown to affect both adult longevity and size (Section 2). These factors may in turn affect fecundity. Therefore, the fecundity of a fourth group of parasitoids was monitored by selecting females from host eggs in which two parasitoids had developed. These females were placed in individual containers. One or two males were then introduced into each container within two hours of the female's emergence and allowed to remain throughout the life of the female.

The temporal distribution of parasitoid oviposition was determined by calculating the mean percent of total offspring produced during each day following emergence from the host egg. The progeny produced by each female received equal weighting regardless of the absolute level of production. If it is assumed that development and survival from oviposition to adult emergence is

constant, then the mean percent of progeny produced during each daily time interval will equal the mean percent of oviposition. Mated females were not segregated according to whether they were known to mate only once or were allowed continual access to males, as this distinction had no apparent relevance to temporal oviposition patterns.

All of the eggs exposed to Patasson n. sp. females that failed to produce either parasitoid adults or carrot weevil larvae were examined under a dissecting microscope at 25x. Any evidence of parasitoid pupae or adults that had died before emerging were credited to the fecundity totals of the appropriate female. However, parasitoid eggs and larvae are small and difficult to see. It is probable that parasitoids which died at an early stage in their development were overlooked.

3.1.2 Oviposition

Host eggs were exposed to newly emerged parasitoid females to determine the age at which oviposition begins. Parasitoids that emerged between 0600 and 0800 h were selected from a laboratory culture. Male-female pairs were placed in clear plastic containers at 0800 h ± 15 min on the day of their emergence. Five carrot weevil eggs less than 24 h old were introduced into each container as described above. At 1000 h ± 15 min these eggs were removed and replaced by a new group of five eggs. This was repeated at 1200 h and at 1400 h ± 15 min. Host eggs introduced at 1400 h were removed at 0800 h ± 15 min the following morning. The host eggs were then individually placed in clear plastic containers and reared at 23° C and the number of parasitoids emerging was recorded.

3.2 Results

3.2.1 Fecundity

The mean number of progeny among all females that developed singly within the host egg was 24.7 (s=32.3). However, one half of these 36 females produced no offspring. The mean for females that produced at least one offspring was 49.4 (s=29.3). The number per female ranged from four to 90.

One of the females that was allowed continuous access to males produced only males among her 17 offspring. Therefore, it was assumed that this female was not fertilized despite the presence of a companion male, and the female was considered to be a virgin in the analysis which follows.

Mating status appeared to have no influence on the fecundity of females that had at least one offspring. The mean numbers of progeny produced by virgin females, females that mated once, and those allowed continual access to males were 41.1, 52.6, and 60.3, respectively (not significantly different, ANOVA, $p>.05$).

Mating status also did not appear to affect the likelihood that a female would produce offspring. Five of 12 virgin females and three of 11 once mated females had no progeny, while 10 of 13 females allowed continual access to males had no offspring.

Superparasitism

The mean number of offspring among females emerged from host eggs in which two parasitoids developed was 22.1 (s=22.6). Twelve of the 18 females examined produced at least one offspring. The number per female ranged from four to 64. The mean for reproducing females was 33.2 (s=19.7) offspring (not

significantly different from the mean for females in all mating status categories which emerged singly from the host egg, t-test, $p>.05$). Although not demonstrated statistically, a relationship between fecundity and superparasitism may still exist since females that developed singly produced an average of 49.1% more offspring than females from host eggs with two parasitoids.

All of the females that developed gregariously and produced offspring were paired with one or two males throughout their adult lives. However, two of these females produced only male offspring. It was assumed that these females (which produced four and 12 offspring) did not successfully mate. Since no significant relationship was demonstrated between fecundity and mating status, all females emerging from two-parasitoid host eggs were considered together, regardless of the sex of their progeny.

The fecundity estimates which have been presented may represent an underestimate of the number of eggs laid by parasitoid females if superparasitism contributed to an increased mortality rate among the immatures. Aeschlimann (1977) reported that mortality among Patasson lameerei was low during development. However, mortality due to larval competition has been observed for several related species (MacGill 1934, Vidano et al. 1979, Statterthwait 1931, Anderson and Paschke 1969).

Among the 7477 carrot weevil eggs monitored, 9.7% were inviable and no evidence of parasitoid or weevil development was found. Of those eggs exposed to parasitoid females that produced at least one offspring, 10.9% were inviable, while only 7.6% inviability was encountered for eggs exposed to females that had no offspring. These values are significantly different (X^2 test, $p<.01$) and suggest that activity by ovipositing parasitoids may have played a

greater role in host egg mortality than was shown by the emergence of adult parasitoids. Competition among parasitoid larvae may have contributed to this additional mortality.

Temporal Distribution of Oviposition

The cumulative temporal distributions of oviposition by all virgin females, all mated females from host eggs in which two parasitoids developed, and all mated females that developed singly are presented in Figure 3. Each of these distributions is significantly different (X^2 test, $p<.01$). Most oviposition occurred during the first four days following emergence at 23° C. Oviposition by mated females from superparasitized host eggs occurred rapidly, and 84.9% of all oviposition by these females was completed within three days after their emergence. Significant oviposition (16.4%) by mated females that developed singly in the host egg occurred during the first day of adult life. Oviposition proceeded at a relatively constant rate through the fifth day following emergence, by which time 86.8% of total oviposition had been completed. No oviposition was observed for virgin females during the first day. Beginning on the second day, oviposition proceeded rapidly and was 94.2% completed by the end of the fourth day.

Sex Ratio

The percent of females among the offspring of once-mated females and females allowed continued access to males was 77.7 and 71.2, respectively (Table 6). These values were calculated by summing the number of progeny of each sex produced by all females in the appropriate mating status category. The

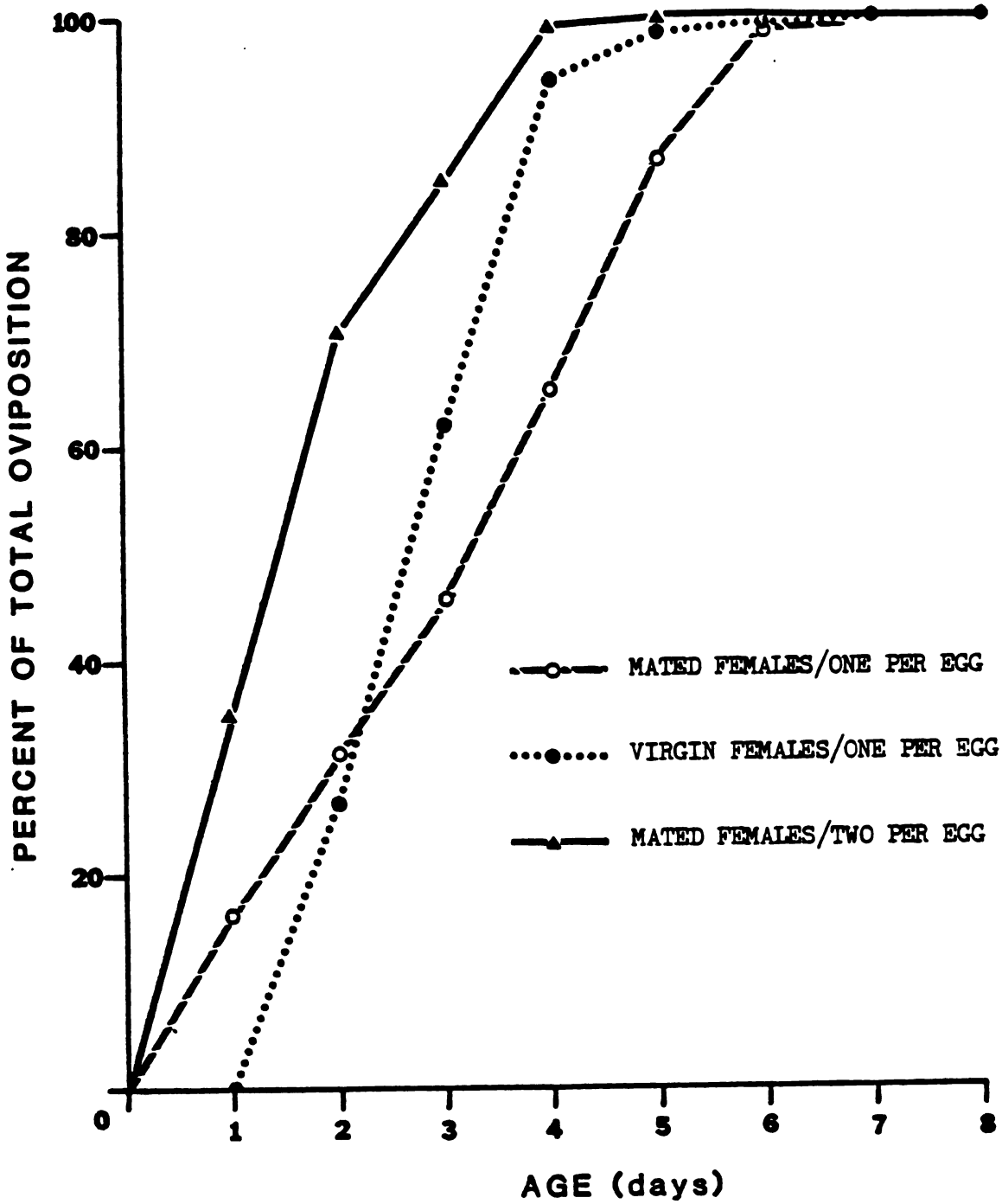

Figure 3. Effect of mating status and number of parasitoids per host egg on the temporal distribution of oviposition by Patasson n. sp. at 23° C.

Table 6. Number of offspring produced by female Patasson n. sp. as influenced by age and mating status of female.

Mating status	Number of offspring produced per day								
	Age of female parent (days)								
	1	2	3	4	5	6	7	8	Total
Female parent mated once[a]									
Total	100	66	81	79	72	15	6	2	421
Females	88	45	68	65	54	7	0	0	327
Males	12	21	13	14	18	8	6	2	94
% Female	88.0	68.2	84.0	82.3	75.0	46.7	0.0	0.0	77.7
Female parent with continual access to males[b]									
Total	220	163	78	74	22	4	2	--	563
Females	182	113	45	50	11	0	0	--	401
Males	38	50	33	24	11	4	2	--	162
% Female	82.7	69.3	57.7	67.6	50.0	0.0	0.0	--	71.2

a. Data represent the offspring of eight females which emerged singly from the host egg.
b. Data represent the offspring of thirteen females which emerged from host eggs from which one or two parasitoids emerged.

contribution made by each female to the total sex ratio was thus weighted by the number of offspring she produced. Females within each mating category were not segregated according to superparasitism.

The percent of female offspring among all mated females was 74.0. This corresponds with sex ratio estimates for closely related species (Anderson and Paschke 1968).

Female progeny were produced by once-mated females for six days after mating had taken place. Total reproduction by both groups was negligible beyond this time (1.0% of the total). This indicates that female parasitoids that mate shortly after emergence are able to store sperm and oviposit fertilized eggs throughout most of their reproductive lives. Since the energy associated with additional mating efforts would not be compensated by any substantial increase in female progeny, it would appear unlikely that females would ordinarily mate more than once.

Number of Eggs Parasitized

The mean number of eggs parasitized per female was 33.3 (s=21.5, n=30). This is more than twice the average number of eggs parasitized by Anaphes flavipes females (Anderson and Paschke 1970a). There were no significant differences among mating status categories in the mean number of host eggs parasitized by females that parasitized one or more eggs (SNK test, $p>.05$). Thus, the mating status of female parasitoids does not appear to affect either the number of offspring or the number of host eggs parasitized. Similarly, no significant difference was shown between the mean number of eggs parasitized by females emerging singly from their host eggs and by females emerging from

superparasitized eggs (t-test, $p>.05$). The mean number of parasitoids per parasitized host egg was nearly equal among all adult categories.

3.2.2 Oviposition

Patasson n. sp. oviposition may begin within a few hours after the emergence of the female. All females examined had emerged between 0600 and 0800 h. One female began to oviposit between 1000 and 1200 h on the morning during which she emerged. Another female began to oviposit between 1200 and 1400 h. The intial oviposition of three females took place between 1400 h and 0800 h on the following day.

No oviposition occurred between 0800 and 1000 h, when host eggs were first made available. However, only five of the 51 females tested parasitized one or more host eggs. Thus, the central tendency of oviposition initiation can not be estimated.

The low rate of parasitism in this experiment may be due to the low number of host eggs used in each trial. When 20-50 host eggs were used in the procedures described earlier, 55.6% of the females produced at least one offspring.

3.3 Discussion

The fecundity observed for mated females was greater than for virgins. However, this difference was not statistically significant. This may be attributable to an inherently high degree of variation associated with individual parasitoid fecundity. Stoner and Surber (1971) obtained a similar result for Anaphes ovijentatus.

Although initial oviposition was delayed, the percent of virgin females that eventually produced offspring did not appear to be different than the percent among mated females. This contradicts the findings of Williams et al. (1951) who observed that only one of 20 virgin Patasson nitens females examined produced offspring. However, Stoner and Surber (1971) reported no disinclination to oviposit by virgin Anaphes ovijentatus females.

Superparasitism was also found to have no statistically significant effect on fecundity even though the mean number of offspring produced by females which emerged singly from the host egg was greater than the mean for females which developed in superparasitized eggs. A relationship between superparasitism and fecundity was observed by Jackson (1961) who attributed the reduced fecundity to the smaller size of females emerging from superparasitized eggs.

Most of the oviposition by both mated and virgin females occurred within 3-4 days of their emergence at 23° C. Mean adult longevity at this temperature was found to be 3.82 days, and survivorship was relatively high during the first few days following emergence, declining rapidly thereafter (Section 2). This suggests that most parasitoid females survive the critical period during which reproductive output is at a maximum, and a large portion of the female population will contribute to the next generation of parasitoids. This is in agreement with the findings of Anderson and Paschke (1970a) who observed that the number of parasitized eggs per female does not increase appreciably with the longevity of the female once they are more than a few days old.

The initiation of oviposition by virgin females appears to be delayed for about a day. The benefits of this strategy would presumably be an increased

likelihood of mating and thus producing female offspring, and hence an increased contribution to subsequent generations per unit of reproductive effort. The opportunity costs associated with the delay would be related to the foregone reproductive output of males and the probability of death during the first day following emergence. By the third day after emergence, the cumulative oviposition of virgin and mated females are approximately equal. The costs associated with longer delays are apparently prohibitive. The delayed oviposition strategy of virgins may also act as a regulating mechanism tending to equilibrate the population sex ratio.

Parasitism of carrot weevil eggs has been observed to occur continuously from early June until the middle of August (Section 8). Parasitoid development was shown to require an average of 11.9 days at 23° C, and mated females complete about 50% of their total oviposition within the first three days after emerging as adults. The average generation time is thus approximately 15 days at 23° C. This suggests that the parasitoid may complete up to five generations during the carrot weevil's oviposition period at this temperature.

The percent of female offspring among once-mated females was 77.7. These females were observed mating within a few hours after their emergence, and the matings were successful since female offspring were produced by each of the adults observed. It is therefore assumed that this is the maximum possible percent of female offspring which will be produced by a field population in which all females have mated. Assuming that total fecundity by virgin and mated females is not significantly different, the percent of virgin females in a field population (V) may be estimated by:

(EQ 3.1) $V = 100 - ((f/77.7) \cdot 100)$

where f represents the observed percent of females among parasitoids emerging from field-collected host eggs. Assuming that the percent of virgin females is related to population density, a relationship could also be derived between the observed sex ratio and field population density. This relationship is based on the assumption that the sex ratio among mated females is uninfluenced by field conditions. However, Flanders (1947) noted that among many parasitic hymenoptera, mated females tend to produce more female offspring at higher host densities. Jackson (1961) observed that the rate of oviposition by mated Caraphractus cinctus females influenced the sex ratio. The effect of environmental factors on the sex ratio among the offspring of mated Patasson n. sp. females is not known. Therefore, the application of the relationship described by Equation 3.1 to field populations may only be useful for relative comparisons of populations assumed to be subjected to similar external influences.

4. Development

Clausen (1940) observed that most mymarids are solitary and only one immature parasitoid usually develops per host egg. However, gregarious development occurs in several Patasson and Anaphes species, including Patasson sp. near sordidatus. No polyembryony has been observed among these genera.

The developmental process and immature stages of several species of Patasson, Anaphes, and related genera have been described (Balduf 1928, Clark 1931, Statterthwait 1931, Jackson 1961, Anderson and Paschke 1969). Development from the egg to the adult stage usually takes 10-15 days. However, development under certain conditions may take considerably longer (Kevan 1946, Bilboni 1970).

Several factors may influence developmental rates. The effects of temperature on development have been reported by a number of observers, including Fisher et al. (1961), Anderson and Paschke (1970a), and Stoner and Surber (1971). Developmental thresholds have been reported for Patasson lameerei by Leibee (1979) and for Anaphes flavipes by Anderson and Paschke (1969).

Developmental time has been found to be influenced by sex (Leibee 1979, Anderson and Paschke 1969), host species (Statterthwait 1931), and relative humidity (Anderson and Paschke 1968). Statterthwait (1931) reported no correlation between the number of Patasson calendrae developing in the host egg and developmental time. However, such a relationship has been observed for some species (Jackson 1961). Variation in developmental time has also been found for different local populations of the same species, and at different times of the year among the same population.

The time required for the development of Patasson n. sp. from the egg to the adult stage is reported here. The effects of temperature, superparasitism, and sex are examined.

4.1 Methods

Patasson n. sp. developmental times were estimated at 17, 23, and 29° C. Groups of 20-50 carrot weevil eggs were exposed to individual female parasitoids for 24 ± 1 h at 23° C. The same egg groups were also used to examine fecundity (Section 3). Each host egg group was then allocated among the three temperature regimes in one of three ways: 1) divided equally into three subgroups with each subgroup reared at a different temperature; 2) 2/3 reared at 23° C and 1/3 at 29° C; or 3) all reared at 23° C. The allocation among temperature regimes for a particular egg group was determined by the availability of space within the environmental chambers used.

The eggs in each subgroup were placed together in a 65 ml clear plastic container with a moistened 5.5 cm disc of Whatman #3 qualitative filter paper. Distilled water was added when necessary to maintain a high relative humidity, and all hatched carrot weevil larvae were removed daily. The eggs in each subgroup were kept in a common container for 4, 6, and 8 days at 29, 23, and 17° C, respectively. Preliminary observations indicated that the expiration of these intervals precedes the earliest possible parasitoid emergence.

After the initial intervals, each egg was placed in a separate container. Eggs were then monitored for parasitoid emergence a minimum of six times per day at 0600, 0800, 1000, 1200, 1400, and 2200 h. Some of these eggs were monitored more frequently to precisely determine emergence times in

conjunction with the procedures described in Section 5. The time interval during which each parasitoid emerged was thus determined and developmental times were calculated.

4.2 Results

Patasson n. sp. development occurs entirely within the host egg. The only preliminary external evidence of parasitism is the appearance of lesions on the host egg surface, which apparently result from penetration by the parasitoid ovipositor. Similar observations have been reported for Gonipterus scutellatus eggs parasitized by Patasson nitens (Clark 1931) and for Agabus bipustulatus L. (Coleoptera: Dytiscidae) eggs parasitized by Caraphractus cinctus (Jackson 1961). Parasitized carrot weevil eggs exposed to Patasson n. sp. females in the laboratory frequently exhibit many such lesions. Five or six lesions may appear on an egg from which only one parasitoid emerges. This suggests that many of the lesions represent unsuccessful attempts at host egg penetration, or that the mortality of immature stage parasitoids is high. The role of superparasitism and parasitoid mortality was discussed in Section 2.

The appearance of these lesions is highly variable and cannot be used as a consistent early indication of parasitism. The first reliable external evidence is the appearance of the red compound eyes of the pupae which are usually visible through the host egg chorion. Pigmentation of the compound eyes as an indicator of pupal stage development has also been noted for several related species (Niemczyk and Flessel 1970, Statterthwait 1931, Kevan 1946, Jackson 1961). Also visible at about the same time are three ocelli, dorsally, and the apically sclerotized mandibles, ventrally. The first appearance of compound

eyes among egg groups took place an average of 11.3, 8.1 and 5.7 days after parasitoid oviposition at 17, 23, and 29° C, respectively. These data give approximations for the length of time required for larval development.

One or two days prior to the emergence of the adult parasitoids, the host egg becomes considerably darkened. Black, pre-emergent adults may be visible at this time. The developmental process is terminated with the emergence of the adult from the host egg.

4.2.1 Temperature

The mean developmental times of Patasson n. sp. at 17, 23 and 29° C were 17.55, 11.93, and 8.68 days, respectively, demonstrating a significant inverse relationship between developmental time and temperature (SNK test, $p<.01$) (Table 7). These data are based on the midpoints of the known intervals in which parasitoid oviposition and emergence occurred. Development took 102% longer at 17° C than at 29° C. The coefficient of variability at each temperature was relatively low, ranging from 10.1% at 29° C to 14.3% at 23° C.

Successful development occurred at each of the temperatures examined. The percent of all eggs exposed to female parasitoids from which adult parasitoids were reared was 47.75, 41.44, and 39.05 at 17, 23, and 29° C, respectively (not significantly different, X^2 test, $p>.05$). These data are based only on egg groups which were allocated equally among the three temperature regimes and in which there was at least one parasitized egg. This implies that the temperature extremes examined do not approach the upper and lower developmental thresholds for this parasitoid.

Table 7. Developmental time of Patasson n. sp. as influenced by temperature, sex, and number per host egg.

	Mean developmental time (h)		
	Temperature (C)		
	17	23	29
No. per egg[a]			
One			
Mean	17.90 a	12.41 b	8.85 d
SD	2.24	1.97	0.82
N	34	458	68
Two			
Mean	16.88 a	11.39 c	8.56 d
SD	1.27	1.17	0.90
N	18	391	58
Sex[a]			
Male			
Mean	16.91 b	12.07 c	8.41 e
SD	1.97	1.82	0.88
N	29	340	69
Female			
Mean	18.36 a	11.84 c	9.00 d
SD	1.79	1.63	0.77
N	23	524	60
Total[b]			
Mean	17.55 a	11.93 b	8.68 c
SD	2.01	1.71	0.88
N	52	866	129

a. In the same row, means followed by the same letter are not significantly different at p=0.01, Student-Neuman-Kuel multiple range test. In the same column, means followed by the same letter are not significantly different at p=0.05, t test.
b. Means followed by the same letter are not significantly different at p=0.05, Student-Neuman-Kuel multiple range test.

4.2.2 Sex

Mean developmental times of females were found to be significantly greater than means for males at both 17 and 29° C, but not at 23° C (Table 7). Although significant in two of three instances, the relative differences in developmental times were small: 8.6, 1.9, and 7.1% at 17, 23, and 29° C, respectively. Sex-based differences in developmental times may thus play only a minor role in field population dynamics.

4.2.3 Superparasitism

Mean developmental times for parasitoids which emerged from host eggs in which one or two parasitoids developed were significantly different only for parasitoids reared at 23° C (Table 7). At this temperature, parasitoids developing singly took an average of 1.0 day longer to develop than those which developed in two-parasitoid eggs. Parasitoids which developed singly also required a somewhat longer developmental time at 17 and 29° C, but the differences were not significant.

4.3 Discussion

Patasson n. sp. development from the egg to the adult stage took an average of 11.9 days at 23° C. Development was shown to be very sensitive to temperature. The high degree of variability under constant temperature conditions reported by Statterthwait (1931) and by Jackson (1961) was not encountered for this parasitoid.

The completion of development was found to occur more quickly among parasitoids which developed in superparasitized eggs at 23° C. Adult longevity

has also been demonstrated to be shortened among parasitoids from superparasitized eggs (Section 2). A field population will generally be composed of individuals which emerged from host eggs in which various numbers of parasitoids developed. Thus, the variation in longevity and developmental times attributable to superparasitism will tend to spread out the emergence and oviposition period of parasitoids originally oviposited on the same day. This may reduce the risks to the parasitoid population associated with a short-term reduction in host egg availability or temporarily unsuitable environmental conditions.

Estimates of developmental times, combined with adult longevity estimates (Section 2), indicate that most of the life of the parasitoid is spent inside the carrot weevil egg as an egg, larva, or pupa. Developmental time as a percent of total longevity is relatively constant. An average of 71.8, 73.4, and 77.4% of the parasitoid's life occurred inside the host egg at 17, 23, and 29° C, respectively, even though the overall length of the life cycle more than doubled as the temperature was decreased from 29 to 17° C (Figure 4). Therefore, most of the life cycle occurs in a relatively insulated environment: inside the host egg, which is in turn inside the plant petiole. This may provide protection from external mortality factors such as low humidity, extreme temperatures, predation, hyperparasitism, and perhaps most significantly from the effects of chemical pesticides. A substantial portion of the total parasitoid population may survive pesticide applications while still inside the host egg even though the adults may suffer high mortality.

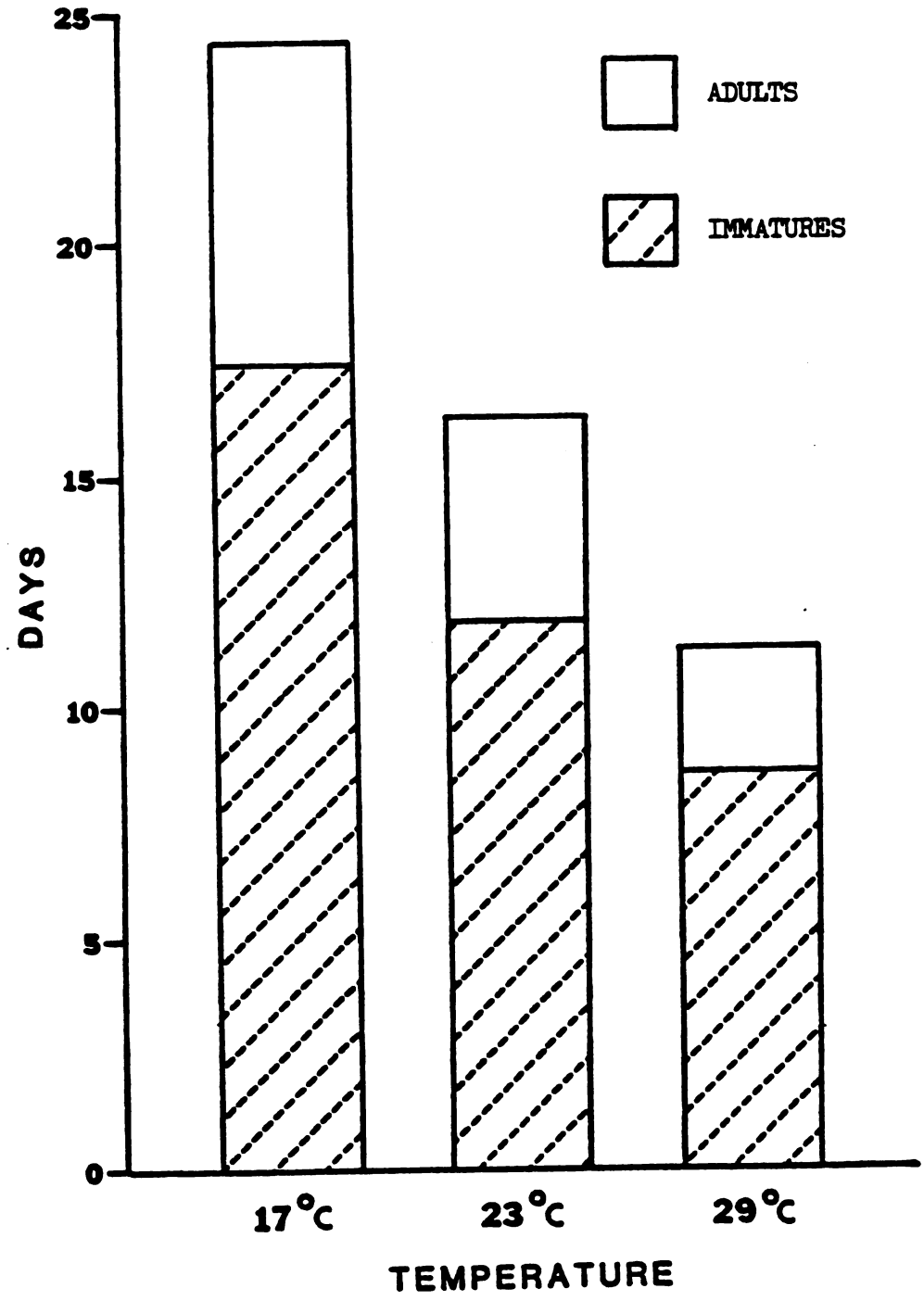

Figure 4. Effect of temperature on the mean duration of the life cycle of Patasson n. sp.

5. Emergence Periodicity

The diel pattern of emergence among Patasson and Anaphes species has received little attention. Emergence usually occurs during the morning. Anderson and Paschke (1970b) suggested that early morning emergence of Anaphes flavipes was related to the high relative humidity which occurs during this time. However, in the laboratory they observed that increases in relative humidity did not always induce emergence, and suggested that a biological rhythm may be involved.

Aeschlimann (1977) observed that A. flavipes males tend to emerge earlier than females. The effect of temperature and superparasitism on emergence patterns has not been reported.

Three experiments were conducted to investigate the temporal pattern of adult parasitoid emergence. The first of these experiments was designed to test for the presence of diel emergence periodicity and to examine the potential roles of temperature and photoperiod. This study provided some evidence of the existence of such a periodicity. A second experiment was designed to more precisely define the dimensions of this rhythm. The final procedure represents an attempt to evaluate the relative roles of endogenous and exogenous factors in the observed periodicity.

5.1 Methods

5.1.1 The Role of Temperature and Photoperiod

Carrot plants were collected from an untreated portion of field #2 at the Hammond Farm on 6 and 8 August 1980. These plants were brought to the laboratory and carrot weevil eggs were extracted. These eggs were randomly

assigned to one of three environmental chambers employing different combinations of temperature and photoperiod: 1) constant temperature of 23° C and constant light; 2) constant temperature of 23° C with a photoperiod of 16:8, photophase beginning at 0600 h; and 3) temperature regime of 26° C for 16 h (0600 to 2200 h) and 20° C for 8 h, with constant light. Two hundred potentially parasitized host eggs were assigned to each of these temperature-photoperiod combinations. Each egg was placed individually in a 65 ml clear plastic container with a moistened 5.5 cm disc of Whatman #3 qualitative filter paper. All eggs were monitored once every eight hours at 0600, 1400, and 2200 h. Parasitoid adult emergence was recorded for each eight-hour interval. Only the first parasitoid emerging from each egg was recorded.

5.1.2 Diel Emergence Pattern

The results of the preceding study indicated that at a constant temperature of 23° C and a photoperiod of 16:8, most parasitoid emergence occurs during the first eight hours of light. The objective of the procedure described here was to more precisely define the parameters of this pattern.

Parasitized carrot weevil eggs were obtained by exposing groups of 20-50 eggs to individual parasitoid females. Egg groups were then allocated among three environmental chambers and reared at 17, 23, and 29° C. All eggs were subjected to a 16:8 photoperiod, with photophase beginning at 0600 h. The same egg groups were also used to examine parasitoid fecundity and developmental times (Sections 3 and 4).

As the developing parasitoids approached the pupal stage (as indicated by the appearance of red compound eyes), the eggs were placed in individual

containers and monitored daily at two-hour intervals during the first eight hours of the photophase (0600, 0800, 1000, 1200, and 1400 h) and again at 2200 h. Adult emergence was recorded during each of these intervals.

Preliminary results indicated that a large portion of parasitoid emergence occurred during the first two hours of the photophase. The emergence pattern was further examined by continuously monitoring some of the eggs during this two-hour interval. Emergence times were recorded to the nearest minute from 0600 to 0800 h for a randomly selected subset of eggs reared at 23° C.

5.1.3 Role of Exogenous Cues

It was hypothesized that adult emergence was cued by photophase. This hypothesis was examined by recording the emergence of parasitoids which were reared under a 16:8 LD cycle, and then exposed to a single extended scotophase just prior to their emergence. If emergence was controlled primarily by an endogenous mechanism, then the scotophase extension should not significantly alter the emergence pattern following entrainment to the 16:8 LD cycle. However, if emergence was primarily controlled by exogenous cues (photophase), then the emergence peak should shift immediately to accommodate the altered photophase.

A subset of the parasitized eggs used in the procedure described above was selected for this experiment. Only eggs reared at 23° C were used. On each day that a trial was initiated, eggs were selected from which the emergence of adult parasitoids was believed to be imminent. These expectations were based on preliminary results of the developmental study which used the same set of parasitized carrot weevil eggs (Section 4). Eggs which had been exposed to the

same female parasitoid during the same 24 h interval were randomly divided into two groups. One group continued to be reared at 23° C with a photoperiod of 16:8, photophase beginning at 0600 h. The second group was placed in a different environmental chamber at 23° C in which the scotophase was extended by two hours, so that it would last until 0800 h. Eggs were exposed to the prolonged 10 h scotophase only once. Developing parasitoids which did not emerge during the photophase which immediately followed the extended scotophase were returned to the original 16:8 light-dark cycle beginning at 2200 h. Subsequent to the day of the scotophase extension, all eggs in both groups were monitored until no further parasitoid emergence occurred. Emergence for both groups was monitored at two-hour intervals from 0600 to 1400, and again at 2200 h.

5.2 Results

Prior to emergence, fully formed adults were often seen moving about within the host egg. A circular exit hole was chewed in the host egg chorion. Once this hole was completed, emergence usually occurred within a few minutes. Parasitoids which developed in the same host egg usually emerged within a few moments of one another. Occasionally the emergence of the last adult from an egg was several hours later than the emergence of the first adult. The newly emerged adults generally remained stationary within 1-2 cm of the vacated host egg and vigorously preened themselves for up to 30 min.

5.2.1 Role of Temperature and Photoperiod

No diel pattern was exhibited by the emergence of parasitoids from eggs reared under constant light and temperature conditions (Figure 5-a, X^2 test, p>

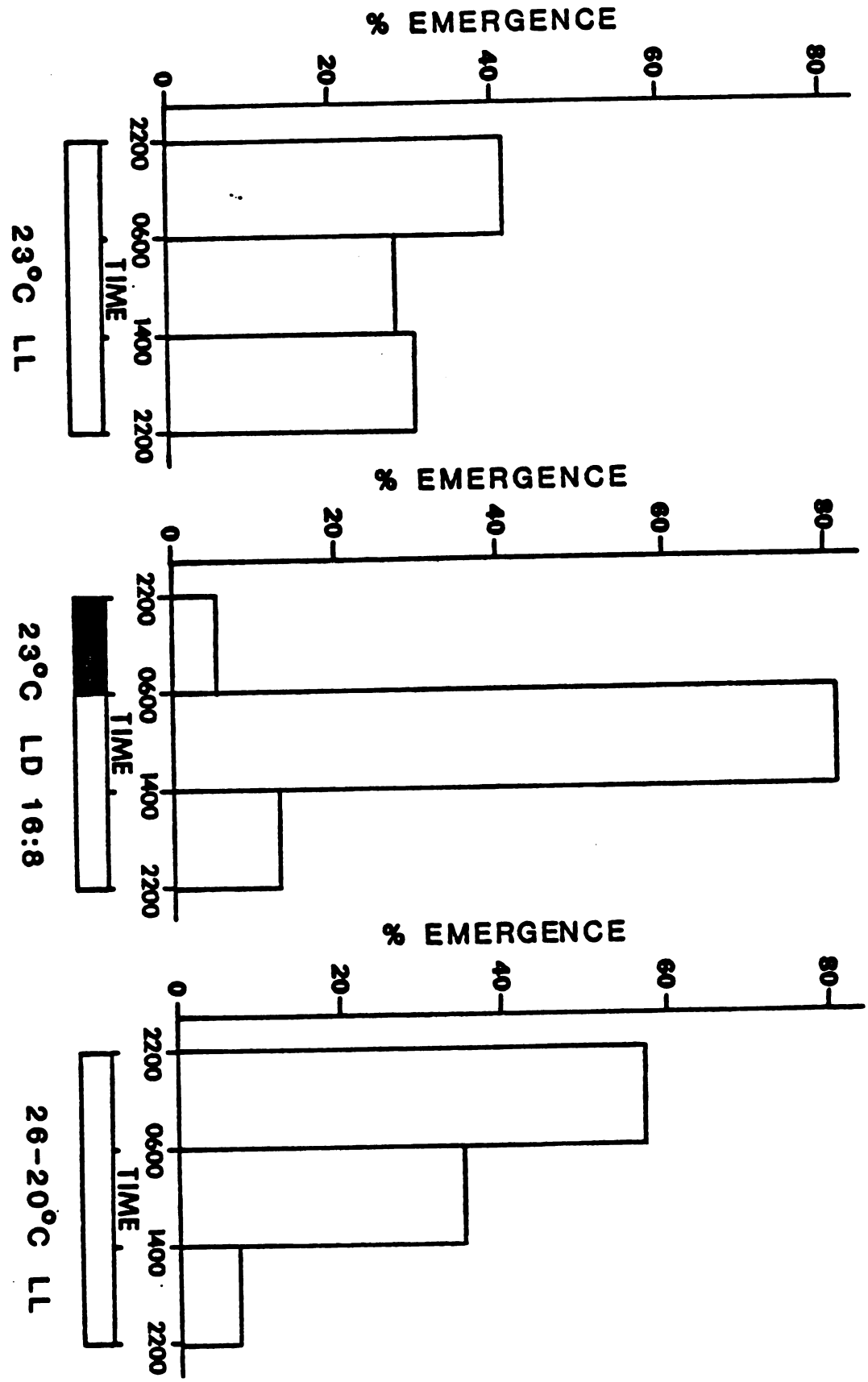

Figure 5. Temporal distribution of emergence from host eggs by Patasson n. sp. in a) contsant light, constant temperature; b) cyclic photoperiod, constant temperature; and c) constant light, cyclic temperature.

.05). A pronounced pattern was found among parasitoids reared under cyclic regimes of either temperature or photoperiod (X^2 tests, $p<.05$).

Over half of the emergence from parasitized eggs kept in constant light and subjected to a cyclic temperature regime occurred during the eight-hour period at 20° C (Figure 5-c). During the first half of the 16-hour period at 26° C, 35.3% of the observed emergence occurred, and only 7.1% occurred during the second half of this period. These results suggest that the lower temperature was more conducive to parasitoid emergence, which would correspond to early morning in the field. Alternatively, parasitoid emergence could be associated with changes in temperature, rather than absolute levels, since both the eight-hour low temperature period and the first half of the 16- hour high temperature period were initiated by 6° C temperature changes.

Parasitoid emergence from eggs reared at a constant temperature and a light-dark cycle of 16:8 occurred predominantly during the first eight hours of the photophase (Figure 5-b). Only 18.5% occurred during the remaining 16 h. These data again suggest that parasitoid emergence may occur in the field during the morning, when temperatures are lower.

5.2.2 Diel Emergence Pattern

A distinct diel pattern was exhibited by the emergence of parasitoids reared at 17, 23, and 29° C with a photoperiod of 16:8. Peak emergence occurred during the first two hours of the photophase, and diminished rapidly thereafter (Figure 6). The percent of total emergence which occurred during the first eight hours of the photophase was 97.2, 81.6, and 79.4 at 17, 23, and 29° C, respectively. This is in close agreement with the pattern described previously

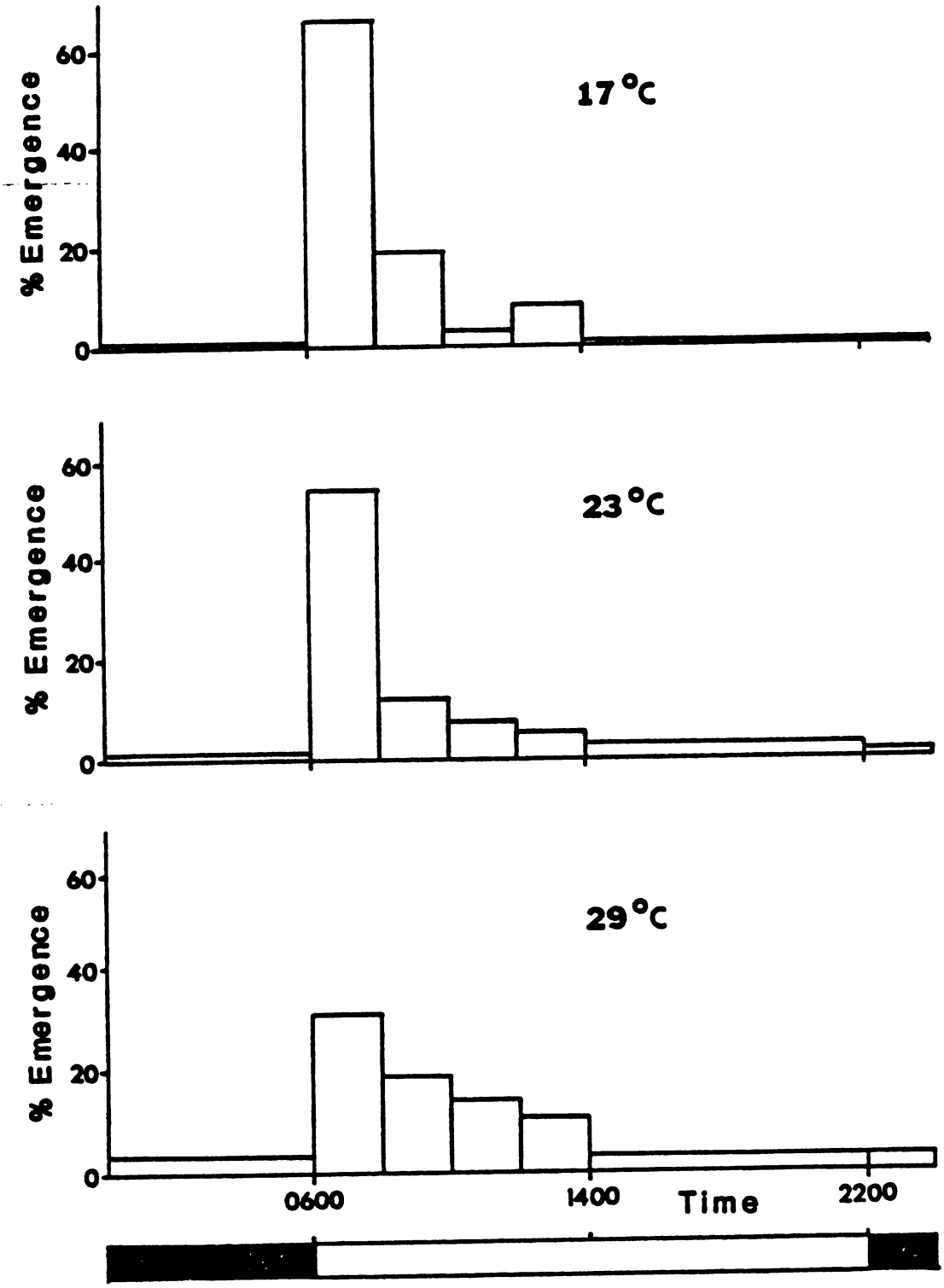

Figure 6. Effect of temperature on the temporal distribution of emergence from host eggs by Patasson n. sp.

for the emergence of parasitoids from field-collected eggs which were reared under the same temperature and photoperiod (Figure 5-b).

Although similar in general form, the relative temporal distributions at each temperature were significantly different from one another (X^2 tests, $p<.05$). Emergence was less concentrated in the first two hours of light at higher temperatures. The percent of emergence occurring during this interval was 66.0, 55.4, and 32.9 at 17, 23, and 29° C, respectively. These data suggest that the effect of photoperiod on emergence periodicity is mediated by temperature.

Superparasitism did not affect the diel emergence pattern. The temporal emergence distribution for parasitoids reared at 23° C which emerged singly was not significantly different than the distribution for those which emerged from host eggs in which two parasitoids developed (X^2 test; $p>.05$).

The diel emergence patterns of males and females reared at 23° C were also not significantly different (X^2 test, $p>.05$). However, among parasitoids which emerged from host eggs monitored continuously from 0600 to 0800 h, males appeared to emerge earlier than the females (Figure 7). One hour after photophase initiation, the number of males reached 59 compared to only 21 females (X^2 test, $p<.01$). After two hours of light, the number of emerged females was greater than the number of males.

5.2.3 Role of Exogenous Cues

The temporal emergence pattern among parasitoids reared at 23° C appears to be controlled by exogenous environmental cues. When the scotophase was extended by two hours, the emergence mode was shifted by two hours (Figure 8-b). The distribution of emergence for parasitoids exposed to the

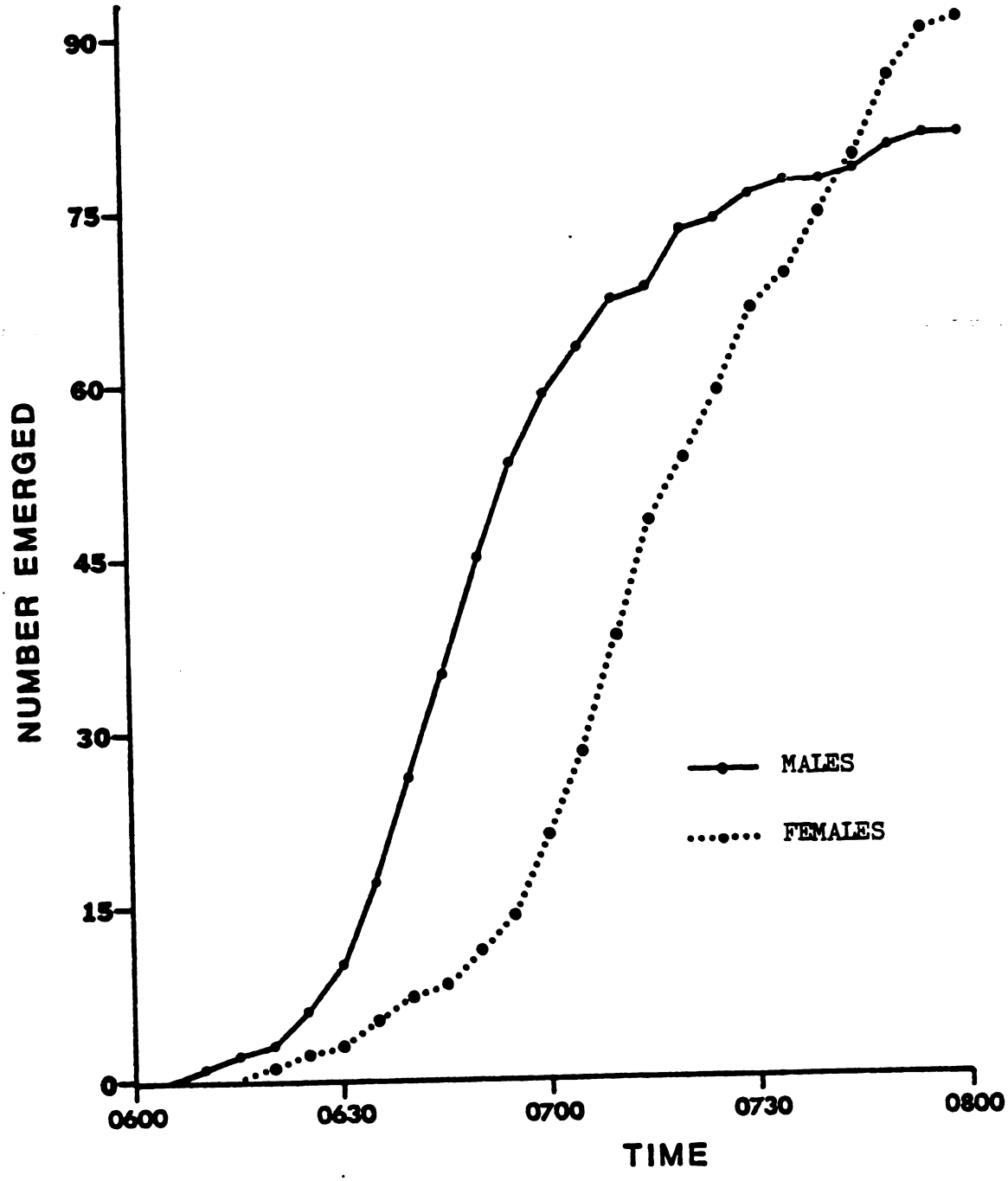

Figure 7. Cumulative emergence from host eggs by adult male and female Patasson n. sp. during the first two hours of photophase at 23° C.

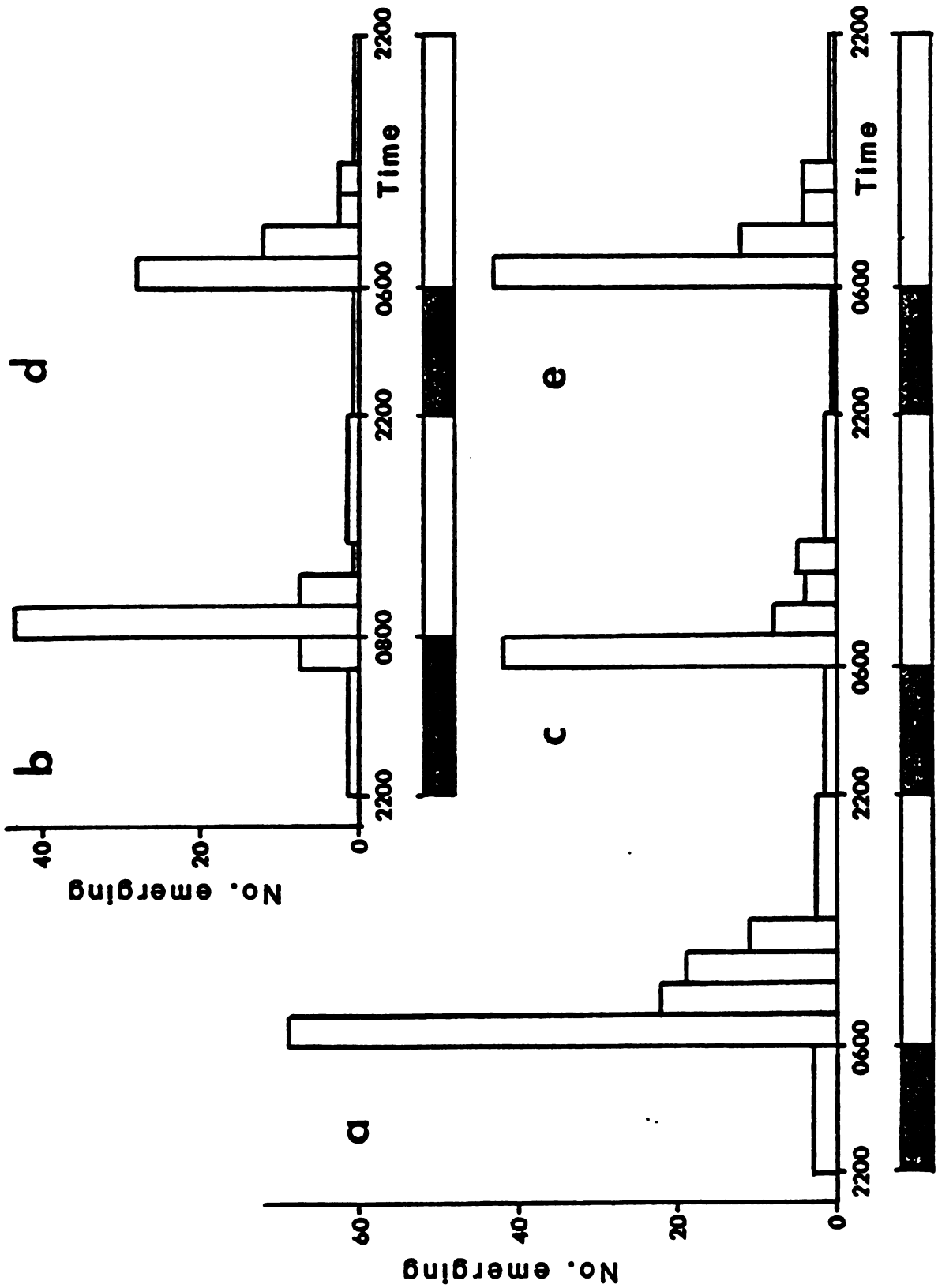

Figure 8. Effect of photoperiod on the temporal distribution of emergence from carrot weevil eggs by adult Pataspon n. sp. at 23° C. Number emerging from all host eggs reared under a photoperiod of LD 16:8 a) on the day prior to a 2 h scotophase extension; from eggs exposed to the scotophase extension on b) the day of the extension, and d) on all subsequent days; and from eggs in a control group on c) the day of the extension, and e) on all subsequent days.

photophase extension was significantly different than the distribution for the control group (Figure 8-c) (X^2 test, $p<.01$).

Saunders (1976) observed that the endogenous nature of a circadian rhythm associated with a particular activity is revealed upon transferring an insect from cyclic to constant conditions if the activity continues to occur at approximately the same time as before. The absence of a residual emergence peak during the interval 0600 to 0800 (which was normally the first two hours of the photophase) suggests that the timing of emergence was immediately shifted to conform to the new environmental conditions. No evidence was found to suggest that an endogenous mechanism caused the emergence rhythm to 'free run' in spite of altered exogenous cues.

Upon returning to the 'normal' 16:8 photoperiod subsequent to the scotophase extension, the emergence peak shifted back to the original time interval. The temporal distributions of parasitoids exposed to the scotophase extension and of parasitoids in the control group were not significantly different (X^2 test, $p>.05$; Figure 8-d & e).

5.3 Discussion

Temperature and photoperiod were shown to influence the emergence periodicity of Patasson n. sp. When parasitized eggs were kept in constant light with a cyclic temperature regime consisting of eight hours at 20° C and 16 hours at 26° C, most emergence occurred at the lower temperature. Most emergence from eggs kept at a constant temperature occurred during the first two hours of the photophase when exposed to a 16:8 photoperiod. This is in agreement with observations made for several related species (Aeschlimann 1977, Anderson and

Paschke 1970b). The association between the initiation of the photophase and peak emergence was greater at lower temperatures.

No relationship was found between superparasitism and emergence periodicity. Sex appeared to have no major effect on the overall emergence pattern, but males tended to appear earlier than females during the first two hours of light. Earlier emergence by males may increase the likelihood that the males will be able to locate conspecific females. Immediately following emergence, both males and females remain relatively stationary for up to 30 min near the vacated host egg and preen themselves. Emerging in advance of the females, the males will be able to complete this activity before the females and begin searching for the stationary females.

Anderson and Paschke (1970b) suggested the possible involvement of a biological rhythm in the emergence of Anaphes flavipes. However, the emergence of Patasson n. sp. appears to be the result of responses to exogenous environmental cues. No endogenous rhythm was demonstrated.

6. Courtship and Mating

The mating behavior of several Patasson and Anaphes species has been described. Mating usually occurs soon after adult emergence, especially among gregarious species in which sibling matings are common.

Males of several species were observed to mate more than once. Anderson and Paschke (1969) reported that the average mating frequency among male Anaphes flavipes was 3.5 times. They suggested that since this corresponds with the sex ratio normally observed for this species, the females were likely to mate only once.

Several studies were conducted in which the courtship and mating behavior of Patasson n. sp. was examined. The first of these studies had two objectives: 1) to observe and describe courtship and mating behavior, and 2) to determine how soon mating can occur after adult emergence. The second study was designed to determine the frequency of mating among male and female parasitoids.

6.1 Methods

6.1.1 Courtship and Mating Behavior

Newly emerged male and female parasitoid pairs were introduced into inverted 65 ml clear plastic containers and their courtship and mating behavior observed. All of the parasitoids used had emerged singly from laboratory-reared host eggs and were thus known to be virgin at the start of the observations. The emergence time of each parasitoid was known so that age at copulation could be recorded.

The courtship and mating behavior of each male-female pair was observed with a 4x hand lens. Components of parasitoid courtship and mating behavior

were identified in preliminary observations. The sequence and duration of components were verbally described and recorded on a cassette recorder for each male-female pair observed. Data were later transcribed from the recordings, and the duration of specific behavioral components estimated with a stop watch.

6.1.2 Mating Frequency

Virgin male and female parasitoids were introduced by pairs into clear plastic containers and observed until copulation occurred. All of the parasitoids used were less than 12 h old when copulation first took place. After mating, each parasitoid was transferred to a separate container. Twenty-four ±2 h later a virgin of the opposite sex was introduced into each of the 20 containers with the previously mated parasitoids. Each of the new virgins had emerged within 12 h of their transfer. Each new pair was observed for 30 min or until mating had taken place. If mating was observed both parasitoids were discarded. If no mating occurred, the introduced virgin was removed and a new virgin was introduced 24 ± 2 h later.

6.2 Results

6.2.1 Courtship and Mating Behavior

Mating by Patasson n. sp. occurs soon after the adults emerge from pupation. Courtship and mating behavior was observed for both males and females within three minutes of their emergence. Sixteen of 26 virgin females examined mated within one hour of emergence, and another eight mated within two hours.

Little overt courtship behavior was observed for Patasson n. sp. females. The female usually remained stationary until the male attempted to mount her, at which time she elevated her abdomen.

Five components of male parasitoid courtship and mating were indentified: 1) general excitation, 2) wing fanning display, 3) antennation of the female abdomen, 4) mounting, and 5) copulation. Each of these components is described below in the order in which they normally occurred.

General Excitation

General excitation of the male usually occurred as soon as a virgin female was introduced into a container with a virgin male. This behavior was manifested by a general increase in movement and by brief, discontinuous bouts of wing fanning.

The wings of Patasson n. sp. are normally held horizontally over the abdomen. During wing fanning the wings were elevated to a vertical position and rapidly vibrated in short bursts lasting ca. 1/3 s each. Wing fanning bouts during the period of general excitation usually involved 1-4 bursts.

The occurrence of this behavior was erratic. It sometimes began within 1-2 s of the introduction of the female, but at other times did not occur at all. The duration of this behavior was also quite variable, and it was difficult to determine when it began and ended.

Wing Fanning Display

Male courtship display was characterized by a relatively prolonged bout of continuous wing fanning, involving up to 37 cycles of wing elevation and

vibration ($\bar{x}$=16.1, $s_{\bar{x}}$=2.0). This behavior was observed only when the male was within 10-15 mm of the female. The average duration of this display was 6.4 s ($s_{\bar{x}}$=1.1). No consistent orientation to the female appeared to be necessary for this display.

Antennation

The male continued the wing fanning display as he moved into a position behind the female. Wing fanning ceased when the antennae of the male made contact with the posterior end of the female abdomen. The abdomen of a receptive female was usually elevated at this time. The male then began to antennate the female's abdomen. Both male and female parasitoids remained stationary during this phase.

Mounting

The male then attempted to mount the female. Receptive females usually remained stationary and mounting was accomplished quickly. Unreceptive females attempted to walk away. The male generally followed, often hanging on to the retreating female. The male continued to antennate the female's abdomen while mounting.

Antennation and mounting occurred so rapidly that estimates for each individual component could not be made. The average duration of the two activities combined was 2.9 s ($s_{\bar{x}}$=0.6)

Copulation

Copulation occurred with the female in a normal standing position, with her abdomen raised. The male leaned back, resting on his outstretched wings and

inserted the aedeagus at the anterior end of the female abdomen (Figure 9). The male often stroked the female's abdomen with his prothoracic legs during copulation. The average duration of copulation was 56.7 s ($s_{\bar{x}}$=11.5). Following copulation, both the male and female usually remained within 10-15 mm of one another and preened themselves for up to 30 min.

The average length of the male courtship sequence, from the beginning of the wing fanning display to the initiation of copulation was 8.8 s ($s_{\bar{x}}$=1.2). Successful mating sequences always involved the wing fanning display, antennation and mounting components, in that order. This sequence was interrupted only by the escape of the female by walking or flying away. If the female managed to get more than 10-15 mm away from the male, the male would revert to the general excitation stage or would cease to exhibit courtship behavior.

6.2.2 Mating Frequency

Male parasitoids readily mated more than once. All of the ten males examined mated with virgin females during each of the first two days following their emergence. Four of five males mated a third time within one hour of previous copulation on the second day.

None of the ten females were observed to mate a second time under the laboratory conditions. Although multiple mating by females under field conditions is not entirely ruled out, it appears to be unlikely. It has been demonstrated that females are capable of producing female offspring for up to six days after mating, and total parasitoid oviposition beyond this age is greatly reduced (Section 3). Therefore, it would appear that no selective advantage would accrue to females that mated a second time to offset the associated time, energy, and risk.

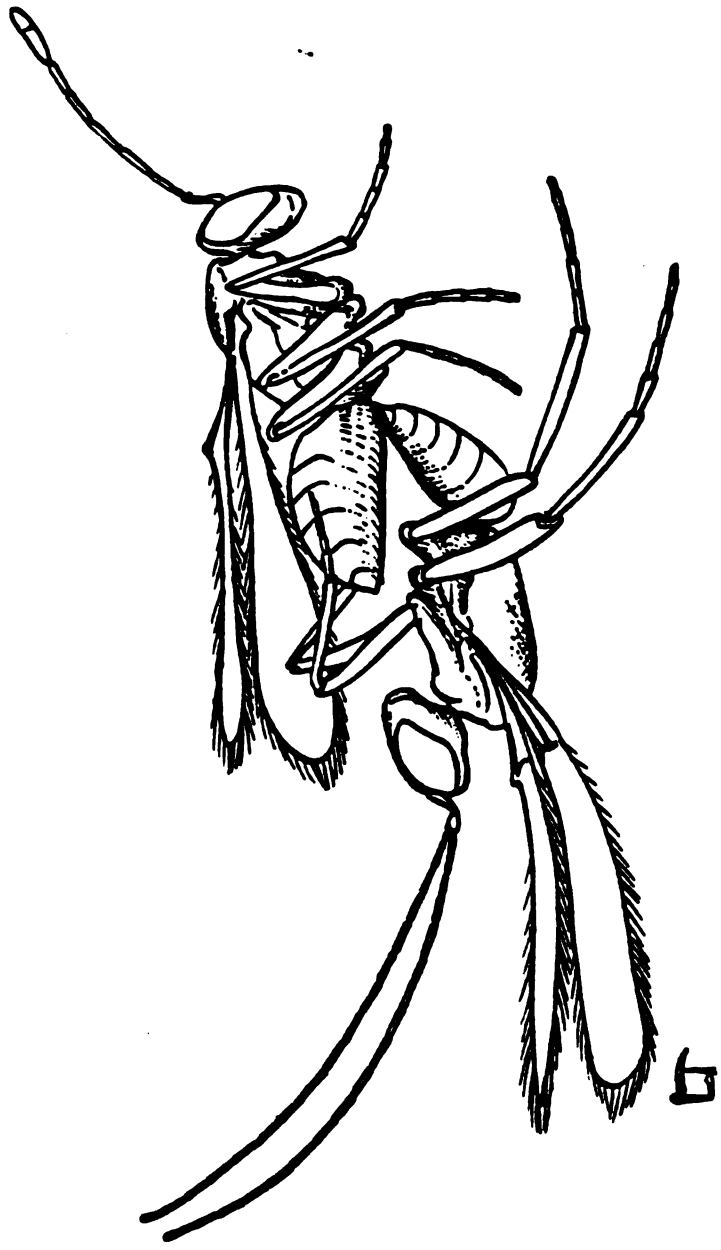

Figure 9. Position of Patasson n. sp. during copulation.

6.3 Discussion

Patasson n. sp. readily mated within a few minutes after emergence from the host egg. Matings were frequently observed between siblings which emerged from the same host egg. Mathews (1975) stated that such matings are common among parasitic Hymenoptera. Similar mating behavior has been observed for other Patasson and Anaphes species (Mossop 1929, Statterthwait 1931, Williams et al. 1951, Aeschlimann 1977). A delay in mating following emergence has been reported only for Anaphes flavipes (Anderson and Paschke 1968).

Dowell and Horn (1975) noted that early, predispersal mating between siblings may tend to lower the genetic variablility within a parasitoid population. A relationship between genetic variability and success as a biological control agent has been suggested (Turnbull and Chant 1961, Simmonds 1963). Force (1967) has also recognized variability as a beneficial attribute of an effective natural enemy. However, Flanders (1947) noted that gregarious parasitoid species generally mate earlier, which results in a more stable sex ratio. This has been supported by observations which suggest that parthenogenic reproduction by virgin females is infrequent among field populations (Kevan 1946, Williams et al. 1951). The advantages associated with a stable sex ratio apparently compensate for the reduced genetic variability among many arrhenotokous species. The importance of a well-balanced sex ratio is apparently reflected in the observed delay in the initiation of oviposition by virgin Patasson n. sp. females (Section 3).

7. Host-Parasitoid Synchrony

Low parasitism rates have been observed among several Patasson and Anaphes species during the early part of the host's oviposition period (Statterthwait 1931, Anderson and Paschke 1968, Bilboni 1964, Dysart 1971, Ellis 1973, Aeschlimann 1977). This could result either from difficulty in surviving periods when primary host eggs are unavailable, or from poorly synchronized host and parasitoid life histories. The degree of synchrony may vary between locations (Mailloux and Pilon 1970) or yearly at the same location (Gage and Haynes 1975).

Carrot weevil adults overwinter in areas adjacent to previously infested fields (Chandler 1926, Wright and Decker 1957). Overwintering may also occur on the crop site. However, when rotation of host and non-host crop plants occurs, the locations of carrot weevil egg populations will change yearly. A concomitant movement by the parasitoid is thus required. Parasitoid dispersal and host-searching abilities have been the subject of many investigations, especially as they relate to the introduction of exotic parasitoid species (Juillet 1960, Hendricks 1967, Anderson and Paschke 1970b, Maltby et al. 1971, Biever 1972). Environmental factors which may influence dispersal include temperature, relative humidity, wind velocity and direction, and crop density.

The objective of this study was to examine the degree of spatial and temporal overlap between Patasson n. sp. and the carrot weevil.

parasitism begins following the intiation of carrot weevil oviposition. Weeds were randomly collected and brought to the laboratory for examination. Carrot weevil eggs were extracted and reared to determine the presence and extent of parasitism.

All weed species present were included in samples collected on 9 May 1980. Carrot weevil eggs were found in only one weed species (Rumex sp.). Subsequent samples taken on 18 May and 4 June included only this weed species.

Parasitoid Overwintering

Overwintering (or aestivation) by several Patasson and Anaphes species takes place in the form of advanced larvae inside the eggs of the primary host (Streams and Fuester 1966, Aeschlimann 1977). The role of carrot weevil eggs in the overwintering of Patasson n. sp. is not known.

Carrot plants were collected in field #2 at the Hammond Farm in an area which had high population densities of both weevils and parasitoids earlier in the season. All plants in a ca. 2 m^2 area were sampled on 26 September 1979, about one month after oviposition by carrot weevils had ceased (Section 8). These plants were taken to the laboratory and examined for the presence of Patasson n. sp. in carrot weevil eggs.

7.1.2 Spatial Synchrony

Carrot plants were collected from the ten western-most seven-row beds of field #2 at the Hammond Farm on 11 July and 1 August 1979, and examined for both carrot weevil infestation and parasitized weevil eggs. Thirty plants were collected from each of the ten western-most beds of the field on each date.

samples of this weed species collected on 18 May, but none were found on 4 June. These data indicate that carrot weevil oviposition began at least as early as 9 May in 1980.

Carrot weevil larvae were reared from all nine of the eggs collected from weed samples; none were found to be parasitized. Parasitism of carrot weevil eggs may not yet have been initiated, or a low parasitism rate coupled with the small size of the sample examined may have prevented detection of sparsely distributed parasitized eggs.

No carrot weevil eggs were found among the weeds collected on 4 June. However, four eggs were collected from carrot plants sampled on the previous day from an adjacent carrot bed (Section 9). One of these four eggs was parasitized by Patasson n. sp. Thus, evidence of parasitism appeared as early as 3 June during the spring of 1980.

Parasitoid Overwintering

No carrot weevil eggs (parasitized or otherwise) were found in 64 carrot plants collected on 26 September 1979, although there was abundant evidence of earlier weevil activity among the plants collected. Carrot weevil eggs thus appear to have no role in Patasson n. sp. overwintering. However, the sample size was relatively small and the possibility that the parasitoid overwinters in carrot weevil eggs at very low population densities cannot be entirely eliminated.

7.2.2 Spatial Synchrony

The total percent of plants infested in the western most 10 beds was 39.3 and 40.3 on 11 July and 1 August, respectively. Weevil activity was more

concentrated along the field margin throughout the growing season. Parasitism rates appeared to be unchanged over space, even though the absolute number of available host eggs decreased toward the field interior. The number of parasitized eggs in each bed on both sampling dates was not significantly different than the number which would be expected if a constant parasitism rate was assumed throughout the 10 beds (X^2 test, $p>.05$).

These data indicate that the parasitoid and host populations were spatially synchronous within the study field. The contribution of the parasitoid to the natural control of the weevil appears to be uniform over the field, and is apparently not affected by host egg density or distance from the overwintering sites.

7.3 Discussion

Carrot weevil oviposition was observed to begin early in May 1980 in the weeds adjacent to a previously infested carrot field. Oviposition on carrots was not observed until early June. Although Patasson n. sp. adults were active in mid-May, parasitism of carrot weevil eggs was not observed until early June. However, the number of weevil eggs examined early in the season was small, so that the relationship between the initiation of weevil oviposition and parasitism could not be determined with certainty.

The coincidence of initial weevil oviposition and parasitism will affect parasitism rates early in the season. This is especially important in celery production where seedlings are transplanted to the field in April in Michigan. If substantial parasitism does not occur until later in the weevil oviposition period it may be too late to significantly influence the level of crop damage.

Environmental conditions may differentially affect the emergence from overwintering of a parasitoid and its host (Gage and Haynes 1975). Thus, the temporal synchrony of early season weevil and parasitoid activities warrants further study under different environmental conditions.

Adult Patasson n. sp. were active in the field several months after the end of the carrot weevil oviposition period. No evidence was found of parasitoid overwintering in carrot weevil eggs. Since overwintering of adults among Anaphes and Patasson species has not been reported, an alternative overwintering host is suggested for this parasitoid.

The mechanism by which Patasson n. sp. overwinters will play a critical role in determining the size of the parasitoid population at the onset of carrot weevil oviposition. The low parasitism rates that have been observed early in the weevil's oviposition period suggest that overwintering may represent a weak link in the parasitoid's life history.

Spring dispersal of overwintering carrot weevil adults appears to occur prior to the initiation of oviposition. When host and non-host crops are rotated, there is little overlap in the year-to-year weevil distributions except in areas adjacent to infested fields. However, parasitism rates were found to be uninfluenced by distance from the field margin during 1979. This suggests that the dispersal abilities of the parasitoid are sufficient to accommodate the yearly shift in spatial distribution by the weevil.

8. Host and Parasitoid Resource Utilization

Carrot weevil oviposition patterns reflect the way in which the weevil exploits available host plants. Host egg availability will in turn influence host finding and exploitation by Patasson n. sp. The objective of this study was to examine the relationship between weevil and parasitoid resource utilization strategies.

Suitable host plants serve as food and oviposition sites for adult carrot weevils, and subsequently as a food source for their larvae. The availability of suitable host plants may represent a major limiting factor on carrot weevil populations in non-agricultural settings. Oviposition strategies determine the efficiency with which the weevil utilizes this resource in producing viable offspring. The manner in which this major resource is exploited is thus of particular interest.

Host plants must reach a certain size or developmental threshold before they are used as oviposition sites by the carrot weevil (Boyce 1927, Wright 1953, Stevenson 1976b). Oviposition ends in late summer or early fall, apparently in response to shortened photoperiod and reduced temperature rather than specific plant conditions (Whitcomb 1965, Stevenson 1976b, Simonet and Davenport 1981). Therefore, this resource may be defined as all suitable host plants which have attained the required size threshold during the weevil's oviposition period.

Carrot weevil egg clutch size is generally low. Observed mean clutch sizes have ranged from 1.3 to 5.0 (Harris 1926, Boyce 1927, Pepper and Hagmann 1938, Wright and Decker 1958, Martel et al. 1976). The number of clutches per plant is also generally low (Whitcomb 1965). This results in a low egg density per plant.

Carrot weevil larval densities per plant are also usually low. In naturally

occurring field populations it is rare to find more than a few late instar larvae per plant. Chandler (1926) reported as many as 2-3 larvae per carrot plant. A similar observation was made by Boyce (1927) on celery.

Several observers have reported instances of higher numbers of larvae per plant. Ryser (1975) reported as many as seven larvae per carrot plant. Wright (1953) found up to 15, and Pepper (1942) reported as many as 22 larvae per plant. However, these observations are difficult to assess, as mean values are not reported. The number of various instar larvae also are not given.

Carrot weevil oviposition patterns were observed during the 1979 growing season in a commercial carrot field. Spatial and temporal relationships were monitored throughout the oviposition period. Egg clutch size and per plant densities were recorded and their relationship to various measures of plant status evaluated. Larval populations were also observed.

Optimal carrot weevil oviposition strategies will maximize the number of surviving offspring per unit of reproductive effort. The carrot weevil is an endemic species. It has presumably evolved its oviposition strategies within a resource array unaffected by man. These strategies may be suboptimal within a commercial agricultural setting. Conditions significantly different than those in which the strategies originally evolved may be encountered. Therefore, an experiment was conducted to evaluate the efficiency of naturally occurring oviposition strategies within the altered resource context represented by a commercial carrot field. The relationship between the survival of larvae and artificially imposed oviposition strategies in the form of various egg densities per plant was examined.

Carrot weevil eggs represent a fundamental resource to the parasitoid

population. Weevil oviposition strategies will determine the spatial and temporal availability of host eggs. The strategies employed by the parasitoid in exploiting this resource will determine the effect of the parasitoid on the weevil population.

Patasson n. sp. resource utilization was examined by observing the relationship between parasitism and host egg clutch size and per plant egg densities. The effect of plant status on parasitism rates, and the spatial distribution of parasitoids were investigated.

8.1 Methods

8.1.1 Field Observations

Carrot weevil egg and larval distribution patterns and parasitism were monitored in an untreated portion of a commercial carrot field during the 1979 growing season. Carrot plants were periodically collected in an untreated area of field #2 at the Hammond Farm near East Lansing in Clinton County, Michigan.

Plant Sampling Procedure

Plants were initially collected on 13 June from the western-most seven-row carrot bed to provide a preliminary estimate of the extent of the carrot weevil distribution. Seven plants were randomly collected every five meters.

Subsequent plant samples were collected from the three western-most carrot beds. All plants within a 1-2 m^2 area in each bed were collected per sampling period. A mean of 115 plants was collected in each bed on each sampling date. The general sampling locations on each sampling date were

randomly selected. Samples were taken from immediately adjacent areas in the three beds. Within each bed, a board was placed perpendicular to the direction of the carrot rows. Retractable measuring tapes were attached to each end of the board, separated by a known distance. As each plant was collected, its location was recorded by noting its distance from the attachment point at each end of the board. The triangular measurements for each plant were later converted to grid coordinates so the precise location of each plant could be determined with respect to all other plants collected within the bed. The approximate area sampled in each bed was estimated by determining the minimum and maximum values for both the x and y coordinates among the plants within each bed.

Carrot Weevil Egg and Larval Data

All plants collected were brought into the laboratory where they were carefully examined for the presence of carrot weevil eggs and larvae. The data collected for each plant included: 1) the number of adult weevils (a rare occurrence), 2) the number of feeding or oviposition punctures, 3) the number of hatched and unhatched eggs in each egg clutch encountered, and 4) the number of each instar larvae found and their location (in the root or foliage).

Plant Data

The total and root fresh weights were recorded for all of the plants sampled. Additional plant dimensions were recorded for a randomly selected subsample of approximately 10%. These data included: 1) the dry weight of the foliage and the root, 2) the length of the taproot and the maximum foliage

height, 3) the maximum diameter of the taproot, and 4) the area of the leaves and stems.

Parasitoid Data

The presence of Patasson n. sp. was not known prior to the 28 June sampling date. Thus, no parasitoid data were available from plants collected on the first three sampling dates. Beginning with plants collected on 28 June, carrot weevil eggs were reared in the laboratory to determine parasitism rates.

A portion of the eggs extracted from plants collected on 28 June were allocated to several clear plastic containers. An average of 37.5 eggs were placed in each container, without regard to their egg clutch or plant source. These eggs were reared at room temperature. The relative humidity was maintained at a high level by periodically adding distilled water to a filter paper disc located in the bottom of each inverted container. The total number of parasitoid adults emerging from these eggs was recorded.

The eggs from each clutch extracted from plants collected on 9 July were reared in a separate container. The source plant for each clutch was known so that parasitism rates could be compared to the available plant dimensions. All containers were monitored daily, and distilled water added when required to keep the filter paper moist. Monitoring of each egg group (clutch) continued until the status of all eggs was determined (i.e., until a carrot weevil larva hatched, a parasitoid emerged, or the eggs were clearly inviable). After extraction from the plant, approximately three weeks were required to determine the ultimate disposition of all eggs. The sex, number, and emergence date for all parasitoids from the eggs in each clutch were recorded. It was also noted whether the

cavity from which the eggs were extracted was sealed with a fecal covering.

The eggs extracted from plants collected on all three subsequent sampling dates were reared individually. This allowed a determination of the number of parasitoids emerging from each host egg.

8.1.2 Survival of Carrot Weevil Larvae

Mechanisms which may account for the low density of late instar larvae which has been observed in the field were examined experimentally by manually transferring various numbers of eggs to plants in an uninfested carrot field, and recording the number of late instar carrot weevil larvae and pupae which successfully developed.

Carrot weevil eggs less than three days old were obtained from a laboratory culture. These eggs were manually transferred to carrot plants within a pesticide-free carrot field located at the Michigan State University Experimental Muck Farm, Bath, Michigan.

The eggs were transferred using a fine bristle paint brush dipped in carrot baby food. The eggs were placed on the carrot plants near the plant base at the junction of two or more stems. The carrot baby food facilitated the adherence of the eggs to the plants. Different per plant egg densities (1,2,4,6,8,10,15, and 20) were randomly assigned to every third row. Two guard rows thus separated the carrots in each treatment (egg density). From five to seven replications (plants) of each density were tested, with all plants within a row receiving the same number of eggs. This procedure was repeated four times at one-week intervals.

The survival of weevil eggs was determined by collecting the plants

approximately three weeks after eggs had been placed on them. The plants were brought to the laboratory and examined for the presence of carrot weevil larvae. The numbers of each instar were recorded. Total and root fresh weights were recorded for all plants.

The soil surrounding the sampled plants was also examined. All soil within 10-15 cm laterally of the plants was collected to a depth of ca. 15 cm. Pupae found in this soil could not be assigned to specific plants, but were allocated proportionally to the plants in the treatment.

The plants in all guard rows and those adjacent to the treated plants were also collected and examined for the presence of carrot weevil larvae. This was done to determine the extent of any larval migration between plants or rows.

8.2 Results

8.2.1 Carrot Weevil Resource Utilization

Larval Density

Per plant larval density remained low throughout the growing season; an average of 1.46 larvae per infested plant was recorded (Table 8). Only 3.78% of the plants had four or more larvae. Similar distributions were found for each larval instar.

Larvae appeared to feed first on the stems in the crown area of the plant. Most first and second instars were found in the foliage (90.2 and 51.4%, respectively). After this food source was exhausted, the larvae moved below ground to feed on the root. Most third and fourth instars were found in the root of the plant (66.4 and 88.8%, respectively). Whitcomb (1965) observed that on smaller carrot plants with 2-4 leaves, the larvae usually go directly to the root

Table 8. Mean per plant density of carrot weevil larvae by larval instar and sampling date, 1979.

	Mean number of larvae per plant							
	Sampling date							
Larval instar	13 Jun	21 Jun	28 Jun	9 Jul	21 Jul	1 Aug	13 Aug	Total
1st instars								
Mean	1.05	1.35	1.28	1.26	1.33	1.29	1.00	1.26
SD	0.22	0.81	0.62	0.60	0.51	0.49	0.00	0.62
N	20	34	46	38	6	7	2	153
2nd instars								
Mean	1.33	1.31	1.00	1.38	1.22	1.00	1.27	1.25
SD	0.58	0.85	0.00	0.83	0.76	0.00	0.47	0.70
N	3	13	11	32	36	6	11	112
3rd instars								
Mean	---	1.50	1.00	1.07	1.27	1.19	1.00	1.19
SD	---	0.71	0.00	0.27	0.59	0.48	0.00	0.49
N	---	2	3	14	41	31	9	100
4th instars								
Mean	---	---	---	1.00	1.26	1.18	1.00	1.19
SD	---	---	---	0.00	0.60	0.39	0.00	0.48
N	---	---	---	5	38	22	10	75
Total								
Mean	1.09	1.38	1.30	1.53	1.77	1.44	1.17	1.46
SD	0.29	0.82	0.66	0.97	1.06	0.66	0.46	0.85
N	23	48	56	73	86	54	30	370

upon hatching and frequently kill the plant. To the extent that smaller plants were killed in this manner and thus excluded from the samples collected, the earlier data may underestimate the proportion of larvae located in the carrot roots.

Fourth instars were not observed until 9 July, and substantial numbers of fourth instars (5% of all larvae) were not observed until 21 July. This suggests that only one complete generation was produced in carrots in 1979. Otto (1978) observed two generations on celery in Michigan in 1977. However, transplanting of celery seedlings into the field usually begins early in April. Therefore, celery plants developed sufficiently to serve as carrot weevil oviposition sites are available in the field much earlier than carrots. Also, the spring of 1977 was exceptionally warm and adult activity was first noted several weeks earlier than in 1979.

Carrot weevil oviposition ceases in mid-August. Thus, weevils produced during the current season on carrots would have little time for their own oviposition. It is assumed, therefore, that most of the oviposition which occurs during a particular growing season is done by adults produced during the preceding year.

Egg Clutch Size

Mean carrot weevil egg clutch size was 1.99 eggs during the 1979 growing season (Table 9). An egg clutch was defined as all eggs, hatched or unhatched, located in the same oviposition cavity. This mean is intermediate to the values reported by Wright and Decker (1958) and by Martel et al. (1976). Clutches ranged from one to seven eggs, but only 9.4% of all clutches had four or more

Table 9. Number of carrot weevil eggs per clutch and per infested carrot plant and the number of clutches per infested plant as affected by sampling date.

Sampling date		No. of eggs / clutch[a]	No. of clutches/ infested plant[a]	No. of eggs / infested plant[a]
13 Jun	Mean	1.49 d	1.29 b	1.93 b
	SD	Ø.69	Ø.64	1.28
	N	28Ø	217	217
21 Jun	Mean	2.ØØ b	1.53 a	3.Ø7 a
	SD	1.Ø2	1.Ø2	2.39
	N	336	219	219
28 Jun	Mean	1.82 c	1.43 a	2.61 ab
	SD	Ø.95	Ø.7Ø	1.75
	N	228	159	159
9 Jul	Mean	2.24 a	1.53 a	3.42 a
	SD	1.17	Ø.89	2.48
	N	22Ø	144	144
21 Jul	Mean	2.2Ø a	1.65 a	3.63 a
	SD	1.15	1.Ø5	2.78
	N	196	119	119
1 Aug	Mean	2.17 ab	1.39 ab	3.Ø2 ab
	SD	1.1Ø	Ø.75	2.Ø7
	N	132	95	95
13 Aug	Mean	2.4Ø a	1.33 ab	3.2Ø ab
	SD	1.Ø9	Ø.68	2.2Ø
	N	8Ø	6Ø	6Ø
Total	Mean	1.99	1.45	2.87
	SD	1.15	Ø.72	2.2Ø
	N	1472	1Ø13	1Ø13

a. In the same row, means followed by the same letter are not significantly different at p=.Ø5, Student-Neuman-Kuel multiple range test.

eggs. Mean clutch size on each sampling date ranged from 1.82 to 2.40 eggs per cavity. Mean clutch size was significantly lower early in the season, but no differences were found among samples collected from 9 July through 13 August (SNK test, $p>.05$). This is the reverse of the trend observed by Niemczyk and Flessel (1970) for Hypera postica wherein clutch size decreased as the season progressed.

Clutches Per Plant

The mean number of clutches per infested plant was 1.45 over the entire period of observation (Table 9). This is somewhat lower than the value reported by Whitcomb (1965). The mean number of clutches per plant was relatively constant during the weevil oviposition period, although the initial mean was significantly lower than the means on several subsequent sampling dates (SNK test, $p<.05$).

Eggs Per Plant

The combination of low mean clutch size and the low number of clutches per infested plant resulted in a low number of eggs per infested plant. The mean number of eggs per infested plant (including hatched and unhatched eggs) was 2.87 for the entire observation period (Table 9). As many as 18 eggs were found on a single plant, but 89.4% of the infested plants had five or fewer eggs. Means for each sampling date ranged from 1.93 to 3.63 eggs per plant. Although significant differences were found, no temporal trend was apparent.

Egg Density and Plant Status

No consistent relationships were found between carrot weevil egg density and plant growth status on any sampling date, as measured by the correlation coefficient between the number of eggs on a plant and maximum foliage length, root length, leaf area, foliage dry weight, and root dry weight. Apparently, carrot weevil oviposition was not affected by the size of the host plant once the plants had reached the necessary size threshold for attack. Among plants sampled on 1 August, significant negative correlations were found between egg density and several measures of plant size. However, this occurred near the end of the carrot weevil oviposition period, and may reflect plant growth inhibition resulting from earlier weevil infestation.

Spatial Distribution

The spatial distribution of carrot weevil eggs within each bed at each sampling was measured by arbitrarily dividing the area sampled into 30 x 30 cm grids and recording the number of hatched and unhatched eggs within each grid. The mean number of eggs per grid and the associated variance was calculated by considering only grids which contained at least one carrot plant (Table 10). The distribution of carrot weevil eggs appeared to be aggregated within grids (as measured by the magnitude of the variances relative to the associated means). Since egg density per plant was low, this distribution may be the result of limited movements by female weevils rather than the spatial aggregation of several females.

The distribution of plants within grids was also somewhat aggregated. A significant correlation was shown between the number of carrot weevil eggs and

Table 10. Spacial distribution of carrot plants and carrot weevil eggs among 30 x 30 cm grids, 1979.

Sampling date	Carrot weevil eggs			Carrot plants			Correlation coefficients[c]	
	Mean	Var.	N	Mean	Var.	N	R1[a]	R2[b]
21 Jun	6.68	47.87	82	5.63	14.06	97	.573 **	-.149
28 Jun	5.62	28.49	61	5.03	6.61	73	.646 **	.097
9 Jul	7.07	55.16	54	4.77	9.53	69	.682 **	.237
21 Jul	6.45	37.65	51	4.42	8.79	64	.592 **	-.102
1 Aug	4.34	23.66	46	3.66	5.48	65	.541 **	-.112
13 Aug	2.86	11.40	40	3.75	5.60	65	.234	-.198

a. Correlation coefficient between number of plants and number of carrot weevil eggs in each grid.
b. Correlation coefficient between the per plant carrot weevil egg density and the number of plants in each grid.
c. Significance at p=0.05 indicated by *; at p=0.01 by ** (F test).

the number of plants per grid as expected, since the mean number of eggs per plant was fairly constant (Table 9). No density-dependent associations were found between the mean number of weevil eggs per plant and plant density.

Carrot Weevil Egg Density and Survival

In the artificial infestation experiment, few carrot weevils successfully developed to reach the third or fourth instar or the pupal stage regardless of the initial egg density. No relationship was found between the number of carrot weevil eggs originally placed on a carrot plant and the subsequent number of larvae and pupae recovered (ANOVA of the raw data and data transformed by $X'=\sqrt{X+0.5}$, $p>.05$). This indicates an inverse relationship between larval survival rate and initial egg density per plant (Figure 10), and suggests the operation of a density-dependent mortality mechanism in the field. A similar relationship was noted by El-Dessouke and Stein (1970) who observed that the survival rate of the weevil Sitona hispidulus was reduced by intraspecific competition at high larval densities.

The destruction of unhatched eggs has been observed to occur in the laboratory as the result of chewing by newly hatched carrot weevil larvae on unhatched eggs. Thus, cannibalism could contribute to the density dependent mortality which was observed.

Although not statistically significant, the average number of larvae and pupae developing per plant increased as initial egg density increased. Thus, optimal oviposition under conditions of scarce resources (e.g., suitable host plants) may shift to a higher per plant density than those which were observed in commercial field situations.

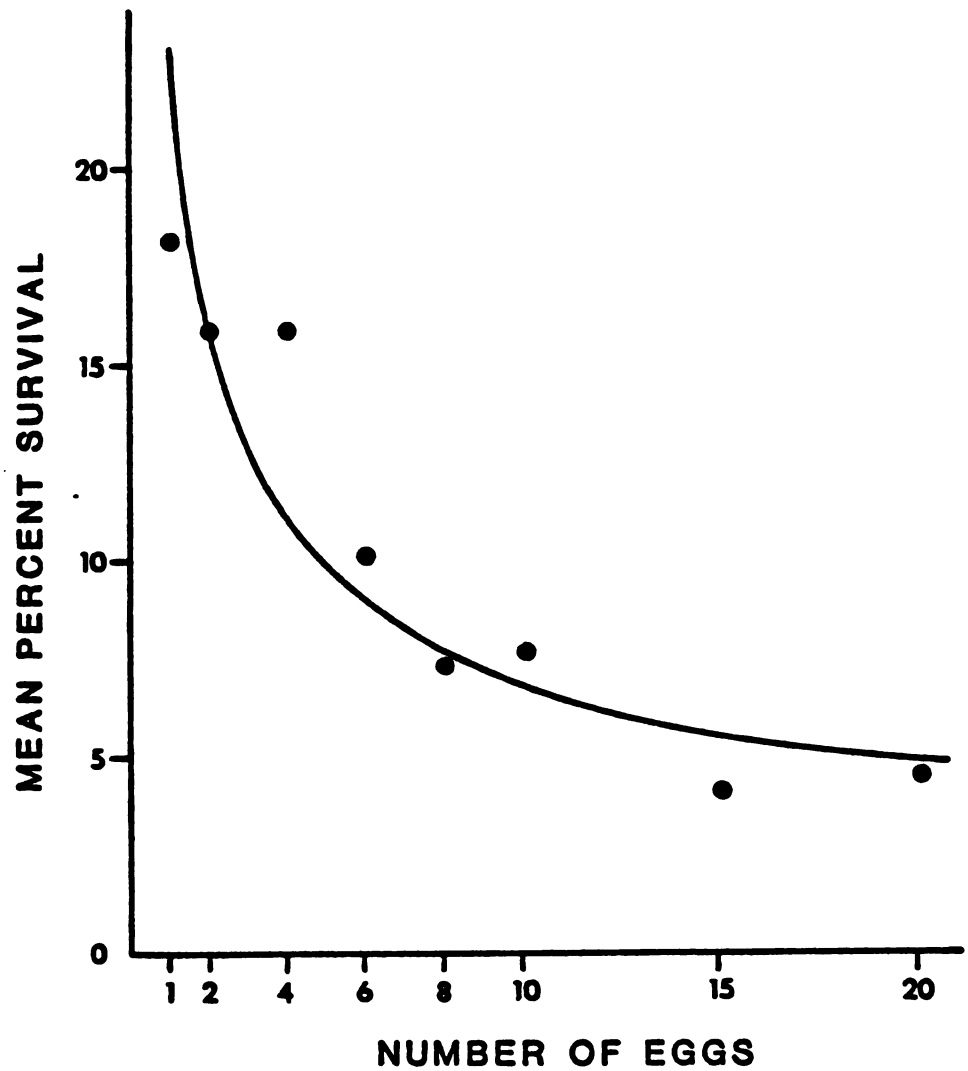

Figure 1Ø. Mean percent of carrot weevils surviving to late instar larvae or pupae after transfer of eggs to uninfested carrot plants ($\log_e Y = -1.47 - Ø.53 \log_e X$, $R = Ø.862$).

Significant differences were demonstrated between the number surviving per plant within each egg density class among eggs transferred on different sampling dates (ANOVA, data transformed by $X' = \sqrt{X + .05}$, $p < .05$). This suggests that survival conditions may change during the growing season in response to plant conditions, weather conditions, or other environmental factors. However, the eggs were transferred under unnatural conditions, so the observed temporal differences may have little relevance to weevil-environmental relationships under more natural conditons. No consistent correlation was found between the number of larvae surviving per plant and several measures of plant size within each sampling date.

No evidence of carrot weevil larval infestation was found in any of the guard row plants. Pepper (1942) and Whitcomb (1965) have reported that the larvae are capable of moving between plant roots. However, such movement appears to be a rare occurrence and may not be a significant factor in larval survival unless it is important early in the season when plants are much smaller.

8.2.2 Parasitoid Resource Utilization

Parasitism Rates

The percent of carrot weevil eggs parasitized during the 1979 growing season was substantial, reaching a peak of 49.32 on 1 August (Figure 11). The average percent of eggs parasitized during the period of observation (28 June to 13 August) was 22.8. These data suggest that parasitism by Patasson n. sp. may have significantly affected the carrot weevil population. In addition, carrot weevil larvae hatched from only 55.77% of all eggs examined, and an additional 21.40% were inviable. Part of the observed inviability may have resulted from undetected parasitism.

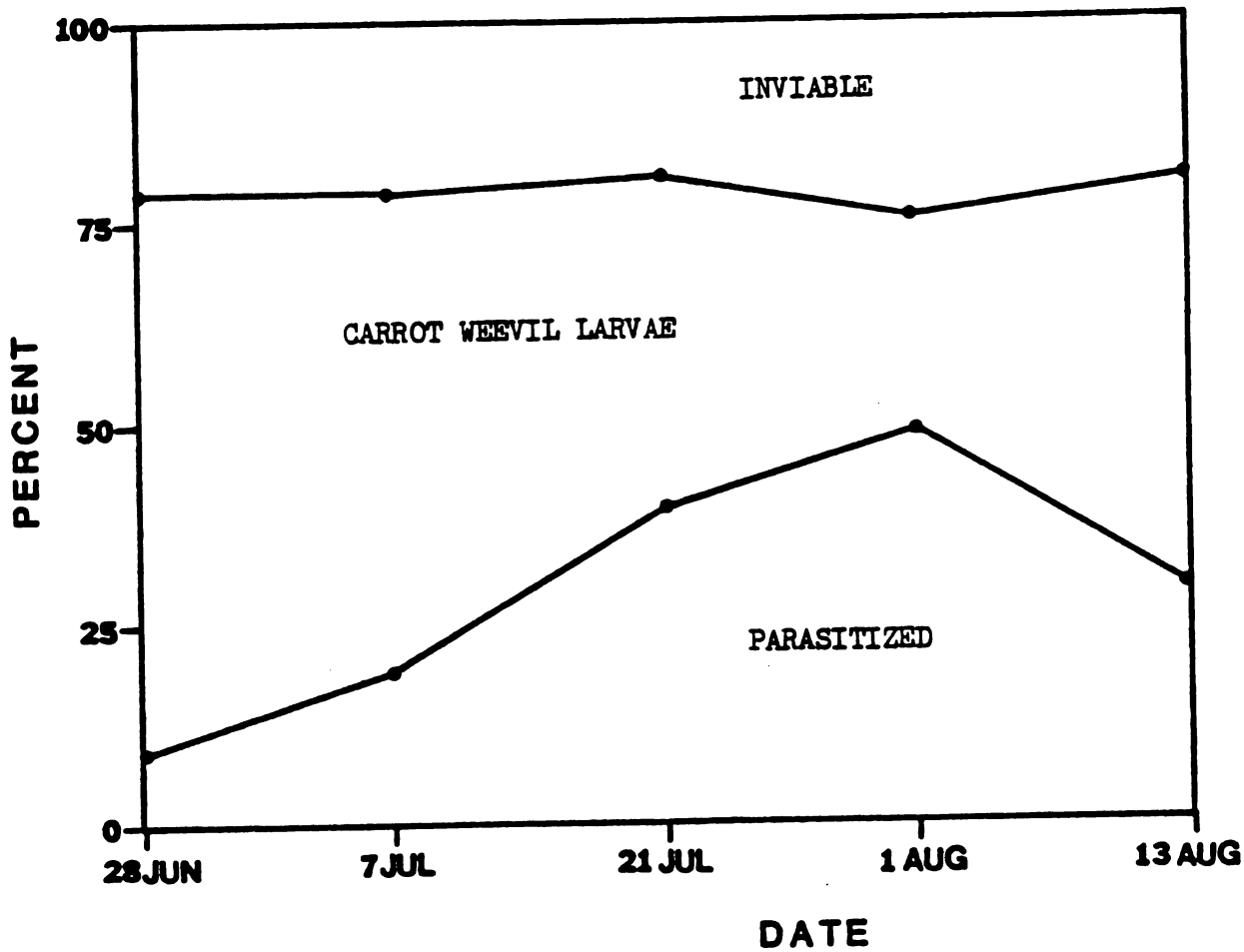

Figure 11. Temporal distribution of parasitism by Patasson n. sp. and inviability of carrot weevil eggs in 1979.

Increased mortality among developing parasitoids has been observed to result from superparasitism (Anderson and Paschke 1969, Jackson 1961, Miller 1966, MacGill 1934). Multiple parasitism may also diminish parasitoid survival. Anderson and Paschke (1969) observed that as the number of Anaphes flavipes females allowed access to a given number of host eggs increased, the number of parasitoid eggs per host egg increased and the survival rate decreased. Early instar parasitoid larvae are difficult to detect. Thus, some of the inviability among carrot weevil eggs may have been the result of parasitoid larvae which themselves failed to develop as a result of high egg density per host.

Parasitoid and Host Egg Density

The density of unhatched carrot weevil eggs declined from 86.3 per m^2 on 21 June to 20.0 per m^2 on 13 August (Figure 12). This decline was apparently unrelated to parasitism by Patasson n. sp. since most or all of the oviposition was attributable to overwintered females. Parasitoid density, as measured by the number of immatures reared from host eggs, increased to 40.5 per m^2 by 1 August, and then declined. On 1 August the number of immature parasitoids per m^2 exceeded the number of host eggs.

The temporal pattern of parasitism by Patasson n. sp. was characterized by a low parasitism rate during late June and early July when host egg densities were highest. Similar trends have been observed for other Patasson and Anaphes species (Statterthwait 1931, Bilboni 1964, Anderson and Paschke 1968, Dysart 1971, Ellis 1973, Aeschlimann 1977). This pattern could be the result of high parasitoid mortality due to either inherent vulnerability to overwintering conditions or a scarcity of overwintering host eggs. Alternatively, the low early season parasitism rates may be the result of inadequate host-finding

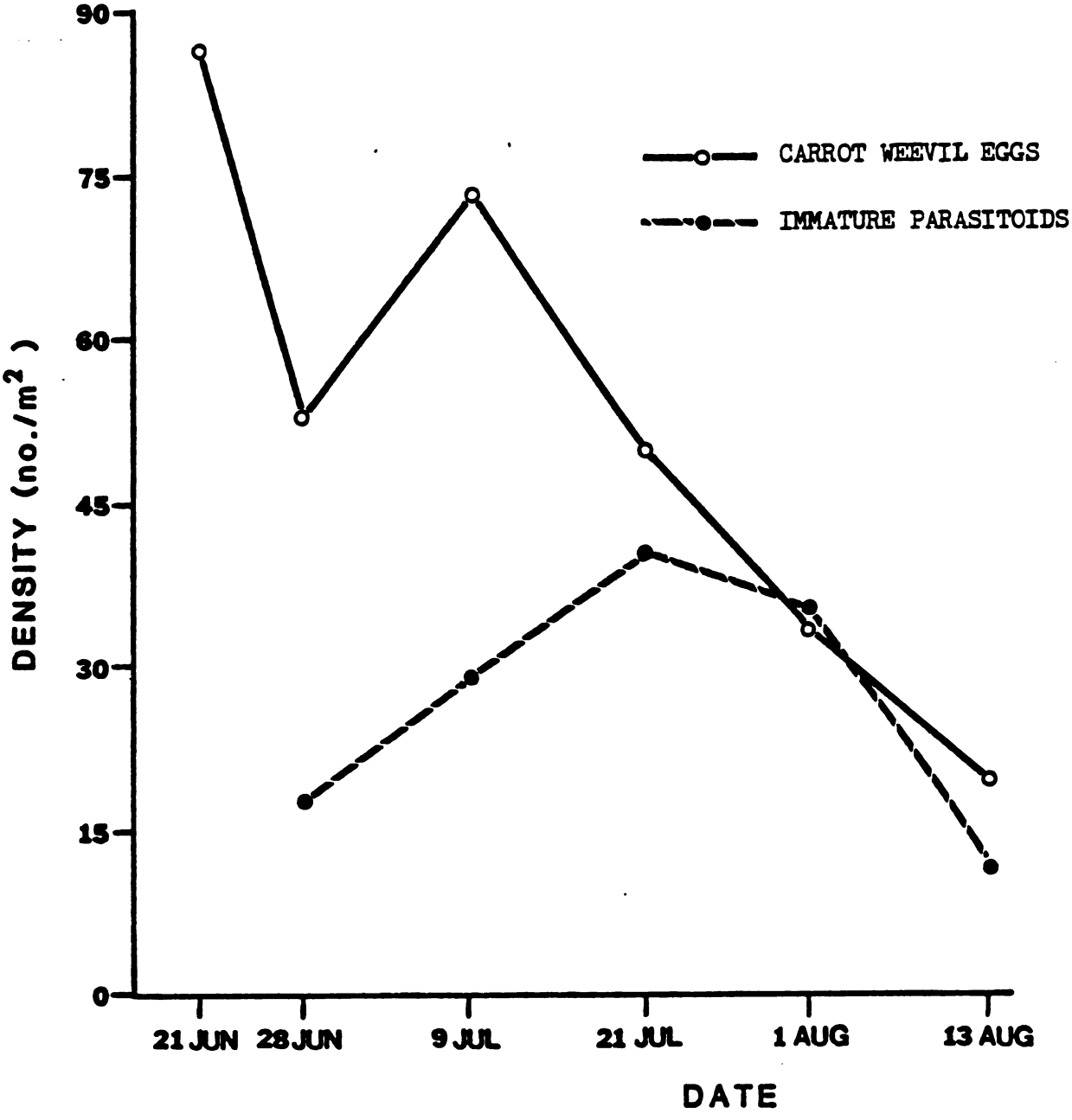

Figure 12. Field density of carrot weevil eggs and Patasson n. sp. immatures within host eggs in Clinton Co., Michigan in 1979.

abilities which are surmounted later in the season only by virtue of greatly increased parasitoid density.

Sex Ratio

Sixty-seven percent of the parasitoids reared from field-collected carrot weevil eggs during 1979 were females, somewhat lower than the percent of female offspring produced in the laboratory by mated females (Section 3). This suggests that a significant fraction of the ovipositing female parasitoids had not mated, which may inhibit rapid population growth. Based on equation 3.1 (Section 3), 13.1% of the females parasitizing the sampled eggs were virgins. This estimate assumes that the sex ratio among offspring produced by mated females in the field was the same as that observed in the laboratory.

The occurrence of virgins among this parasitoid population appears to be higher than has been observed for other species. Kevan (1946) noted that reproduction by virgin Patasson nitens females was rare. Anderson and Paschke (1968) found evidence of oviposition by virgin Anaphes flavipes females in only one of 87 parasitized eggs examined.

Although not statistically different (X^2 test, $p>.05$), the percent of females increased from 59.7 among adults reared from eggs collected on 9 July, to 74.5 on 13 August. Thus, the estimated frequency of virgin females decreased from 22.9% to 4.1% (based on equation 3.1, Section 3).

The sex ratio of parasitoids emerging from host eggs collected in the field on a given date reflects the mating status of the parental adults at some earlier date. Assuming that the parasitoid life cycle requires about two weeks in the field (Section 4), the sex ratio reported for parasitoids emerging from eggs

collected on 13 August would be a reflection of the mating status of parasitoid adults in the field during the preceeding two weeks. Therefore, the maximum percent of mated females in the field appeared to have occurred around the time of maximum parasitoid density. This suggests a relationship between population density and the frequency of mating. This relationship could be useful in the derivation of population density estimates.

Parasitism and Access to Host Egg Cavities

The fecal plug with which the female carrot weevil covers the oviposition cavity had no effect on parasitism. Among eggs collected from 9 July to 13 August, parasitism of eggs from cavities which were covered with a fecal plug was 40.1%, while parasitism of eggs from unsealed cavities was 40.9%. The fecal plug thus appears to have no inhibitory effect on the parasitoid, nor does it appear to enhance host location.

Parasitism and Host Egg Clutch Size

Parasitoid host finding was not influenced by host egg clutch size. No significant differences were found in the percent of clutches parasitized within clutch size categories (X^2 test, $p>.05$). Thus, the probability that a clutch will be located by a parasitoid female is not affected by clutch size.

Parasitoid oviposition behavior was also uninfluenced by clutch size. No differences in the observed degree of superparasitism were attributable to clutch size (X^2 test, $p>.05$). Similarly, the percent of eggs parasitized within a clutch was unrelated to clutch size. Thus, once a clutch was located by a female parasitoid, her treatment of individual host eggs was unaffected by the number of eggs available.

The number of parasitoids which emerged per host egg remained nearly constant, increasing from 2.18 among eggs collected on 21 July to 2.33 on 13 August (not significant, X^2 test, $p>.05$). Thus, the degree of superparasitism was relatively constant, even though relative parasitoid and host egg densities varied greatly (Figure 12).

Parasitism and Per Plant Egg Density

The number of available host eggs per carrot plant appeared to have no effect on parasitism. The percent of plants with one or more parasitized eggs was not related to host egg density per plant (X^2 test, $p>.05$). Similarly, egg density per plant had no significant effect on the number of parasitoids which emerged per parasitized egg or the percent of available eggs parasitized among parasitized plants. Plant size also had no apparent effect on parasitoid host finding or oviposition behavior. No significant correlations were found between total plant fresh weight and the number or percent of parasitized host eggs (F tests, $p>.05$).

These data indicate that the probability that a plant with host eggs will be found was not affected by egg density per plant, and that once a plant with host eggs was located, parasitoid oviposition behavior was not influenced by the number of eggs available. Therefore, the absolute number of parasitoids and parasitized eggs per plant was determined by the number of eggs available (Figure 13).

Spatial Distribution

The spatial distribution of parasitoids was examined by recording the number of adults that emerged from carrot weevil eggs collected within

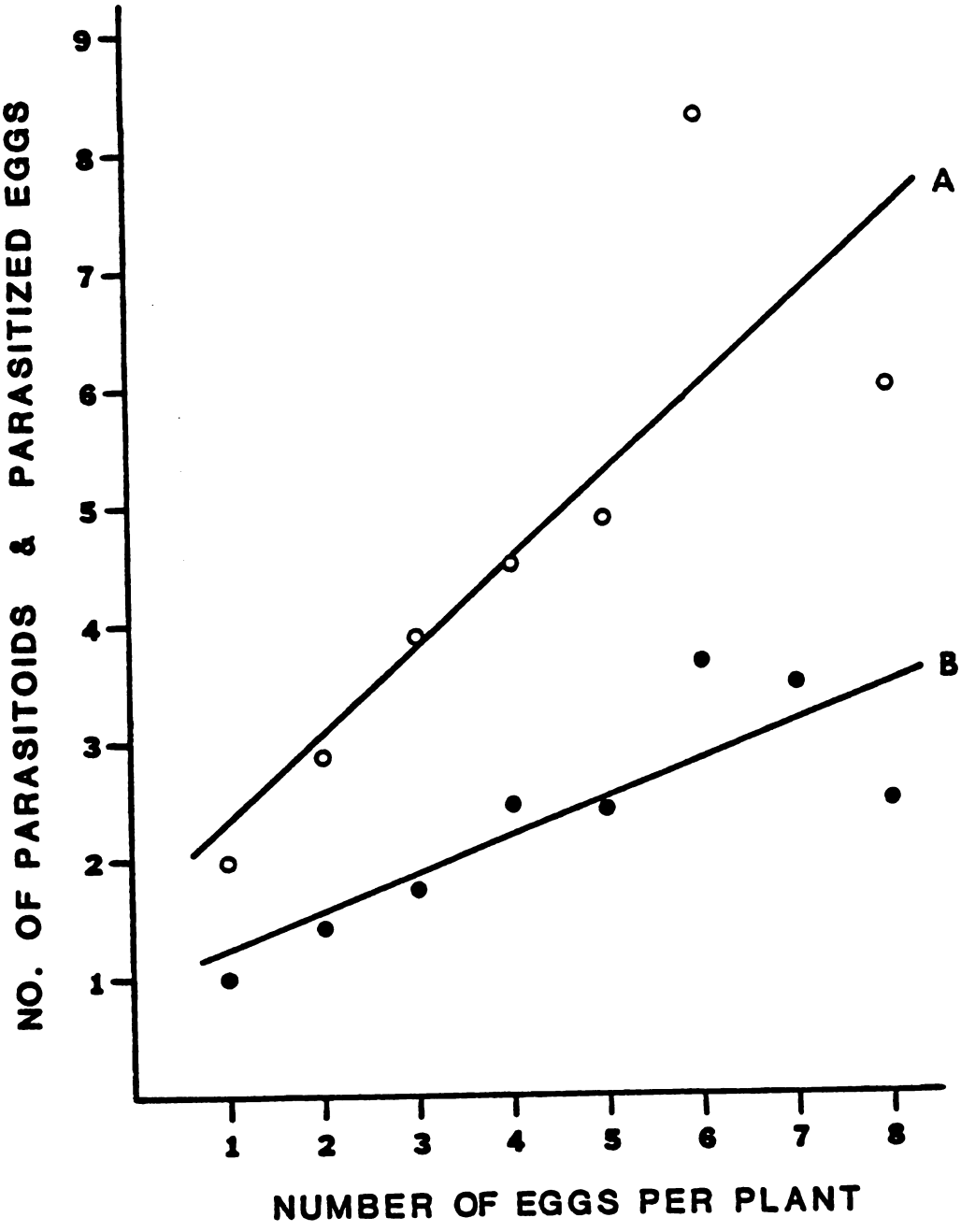

Figure 13. Effect of per plant host egg density on a) mean number of Patasson n. sp. (o) (y = 1.64 + Ø.73 X, R = Ø.718), and b) mean number of carrot weevil eggs parasitized per plant (●) (Y = Ø.92 + Ø.32 X, R = Ø.685).

arbitrarily designated 30 x 30 cm grids. The distribution of parasitoids appeared to be aggregated when all grids were considered, as well as when grids with one or more host eggs were considered (Table 11). However, this is primarily the result of the aggregated distribution of host eggs, as shown by the highly significant correlations between the number of parasitized eggs and the number of available host eggs per grid. The distribution of parasitized eggs was more random at the end of the carrot weevil oviposition period when host egg density was low and approached a random distribution itself.

Parasitism rates were generally not dependent on host egg density (Table 11). A significant correlation between the percent of eggs parasitized and egg density was found on 1 August. However, this relationship explained only 10.2% of the observed variation in parasitism rates.

8.3 Discussion

8.3.1 Carrot Weevil Resource Utilization

Carrot weevil oviposition was characterized by small clutch size and low egg density per plant. Plant status appeared to have no influence on oviposition. Egg populations were spatially aggregated, but this aggregation was not related to host plant density.

Density-dependent mortality (presumed to result primarily from cannibalism) was shown to occur when different carrot weevil egg densities were experimentally imposed on carrot plants. In naturally occurring field populations, much of this density-dependent mortality may be avoided by low egg densities per plant. This pattern of oviposition may represent an adaptive strategy which originally evolved to efficiently exploit the weevil's naturally

Table 11. Spacial distribution of carrot weevil eggs parasitized by Patasson n. sp. among 30x30 cm grids, 1979.

Sampling date	Mean number of parasitized eggs per grid						Correlation coefficients[c]	
	All grids			Grids with host eggs				
	Mean	Var.	N	Mean	Var.	N	R1 [a]	R2 [b]
9 Jul	0.768	1.534	69	0.982	1.754	54	.550 **	-.126
21 Jul	1.172	3.954	64	1.442	4.487	52	.434 **	.051
1 Aug	1.092	3.929	65	1.544	4.876	46	.803 **	.320 *
13 Aug	0.323	0.472	65	0.525	0.660	40	.378 *	-.066

a. Correlation coefficient between the number of available host eggs and the number of parasitized eggs in each grid.
b. Correlation coefficient between the percent of parasitized eggs and the number of available host eggs in each grid.
c. Significance indicated by * at p=0.05 and ** at p=0.01, F test.

occurring host plants. Wild host plants have a much smaller taproot, and unlike commercial plant varieties, may be unable to support a large number of larvae. The observed field oviposition pattern may thus avoid much of the wasted reproductive energy expenditure which would be associated with greater egg densities per plant.

Low carrot weevil egg densities may not always occur. Celery collected near Hudsonville, Michigan, in July of 1980 had an average of 17.1 eggs per plant ($s=13.9$, $n=14$). Clutch sizes appeared to be comparable to those found on carrots. The greater egg density may thus be attributed to a larger number of clutches per plant.

The higher egg density on celery may be the result of differences between the two plants. These differences could be based on qualitative suitability, or on quantitative differences such as root size and extent of foliage. However, quantitative differences among carrot plants were found to have no effect on egg densities.

Alternatively, the observed egg density differences may be attributable to differences in the density of ovipositing female weevils. Celery is transplanted into the field in April in Michigan. Thus, suitable host plants are usually available in the field when spring weevil activity begins. This may tend to limit dispersion, resulting in increased density. This appears to be the more probable explanation as there is no evidence that celery is utilized differently than carrots by similar densities of adult weevils.

No evidence is available concerning the survival of larvae on celery. However, it is assumed that the density-dependent mortality manifested on carrots would function on celery as well. This implies that reproductive efficiency would decrease as the population density increased.

Carrot weevil oviposition behavior has presumably evolved to efficiently utilize more spatially diffuse resources than are encountered in a monoculture of commercial carrots or celery. The likelihood of dense aggregations of adults following spring dispersion would appear to be diminished in a resource array unaltered by man.

8.3.2 Parasitoid Resource Utilization

No relationship was found between the parasitism rate and clutch size or host egg density per plant. Parasitism was also unaffected by plant size. The spatial distribution of parasitized carrot weevil eggs was aggregated, and appeared to be determined by the host egg distribution.

Turnbull and Chant (1961) observed that the relationship between the pest species and the affected crop greatly influences the effectiveness of a parasitoid species in preventing economic damage. A single late instar carrot weevil larva is generally sufficient to render a carrot plant unmarketable. It has been demonstrated that only a few carrot weevil larvae will develop per plant regardless of the initial number of eggs. Therefore, virtually all of the carrot weevil eggs on a plant must be parasitized to avoid economic injury.

An effective parasitism rate may be defined as the percent of plants in which all carrot weevil eggs are parasitized, thereby preventing larval damage. The probability that a particular egg will be parasitized is unaffected by egg density per plant, and is independent of the status of other eggs in the clutch. Thus, the effective parasitism rate (EPR) for a given nominal parasitism rate (i.e. the overall percent of eggs parasitized), and a given distribution of plants among weevil egg density categories can be estimated by:

$$\text{(EQ 8.1)} \qquad EPR = \sum_{i=1}^{k} (P_i \cdot NPR^i) \Big/ \sum_{i=1}^{k} P_i$$

where P_i is the number of plants in egg density category i, NPR is the nominal parasitism rate, and k is the number of density categories.

The relationship between the nominal and effective parasitism rates can be calculated for any carrot weevil egg density distribution. Using the distribution for the entire period of observation during 1979, the relationship would be as depicted as in Figure 14. At lower parasitoid population densities, the parasitoid is relatively ineffective at preventing damage to the carrot plants. At higher densities the effective rate will more closely approximate the nominal rate.

During the entire 1979 observation period, 22.8% of all carrot weevil eggs were parasitized. The effective parasitism rate during this period was only 8.5%. Estimates of effective parasitism rates were made based on observed carrot weevil egg distributions for each sampling period (Table 12). These estimates conform closely to the observed percent of plants in which all available host eggs were parasitized.

The effective parasitism rate has been defined in terms of the percent of plants in which all eggs were parasitized, but it also applies to the survival of carrot weevil larvae. As only one or occasionally two larvae will generally complete their development on a single plant, the effect of parasitism on the next generation of weevils will also be related to the number of plants in which all available eggs have been parasitized. Carrot weevil oviposition patterns are characterized by low per plant egg densities, which may represent an adaptation for optimizing the number of offspring per unit of reproductive effort. However, as parasitoid oviposition appears to be distributed independently of host egg

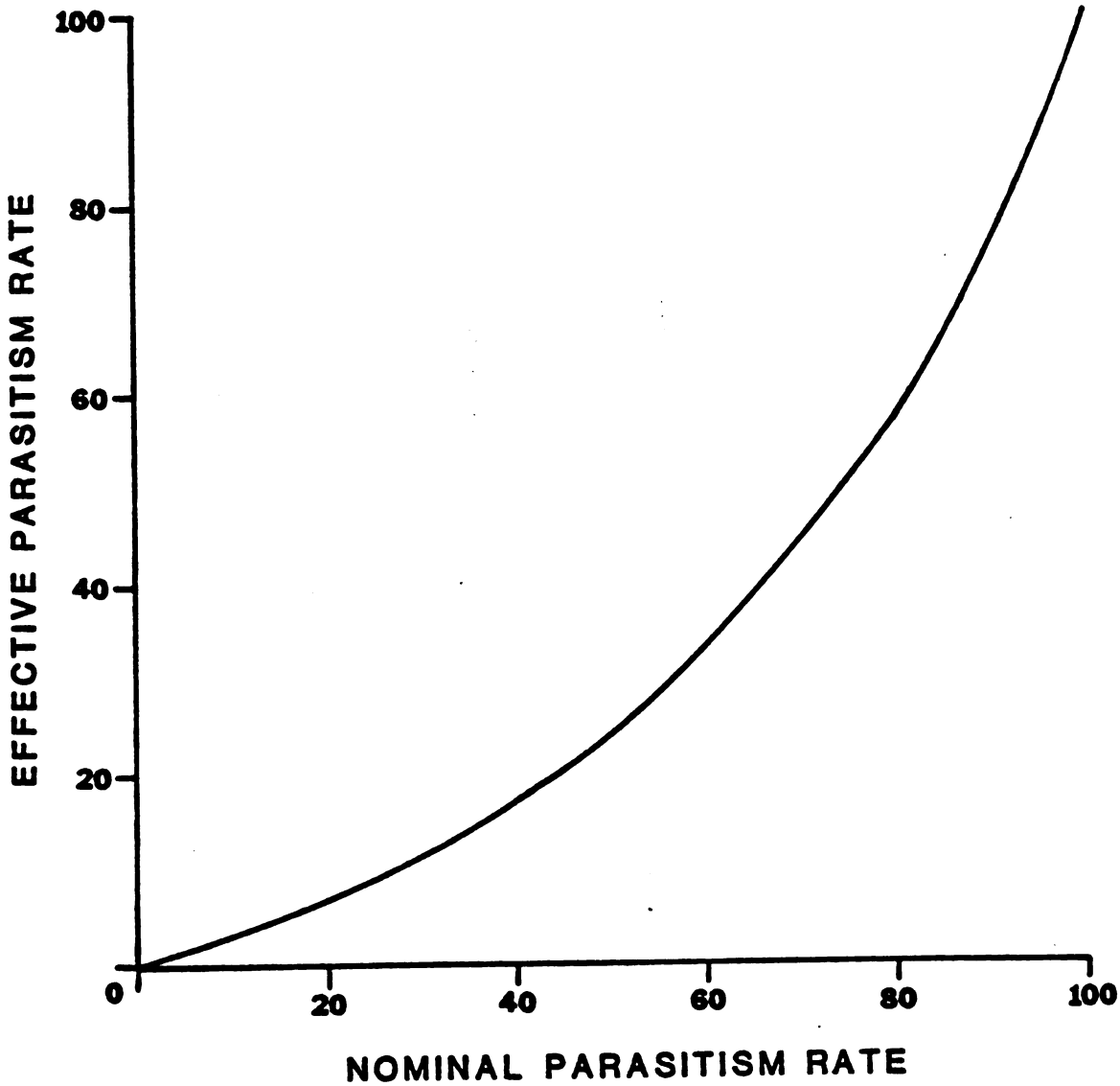

Figure 14. Relationship between nominal and effective rates of parasitism of carrot weevil eggs on carrots by Patasson n. sp. for a given distribution of host eggs per plant. (Nominal rate = percent of eggs parasitized; effective rate = percent of plants in which all eggs are parasitized).

Table 12. Nominal and effective rates of parasitism by Patasson n. sp. in 1979.

Sampling date	Nominal para. rt.[a]	Effective parasitism rate[b]	
		Estimated	Observed
28 Jun	9.35	3.34	---
9 Jul	19.ØØ	5.Ø7	---
21 Jul	39.41	13.76	14.92
1 Aug	49.32	21.92	18.37
13 Aug	29.63	8.38	14.71

a. Percent of carrot weevil eggs parasitized.
b. Percent of infested carrot plants in which all carrot weevil eggs are parasitized.

density, lower egg densities per plant will increase the inhibitory effect of the parasitoid on the weevil population.

Several additional factors may influence the effectiveness of a parasitoid as an agent of biological control. The destruction of parasitized host eggs by newly hatched carrot weevil larvae would reduce the parasitoid population growth rate. Barton and Stehr (1970) observed that newly hatched Oulema melanopus larvae do not interfere with eggs parasitized by Anaphes flavipes. However, newly hatched carrot weevil larvae were observed to occasionally destroy other carrot weevil eggs in the laboratory. Presumably, parasitized eggs could also be destroyed. The frequency at which this phenomenon occurs is not known.

Simmonds (1948) observed that the value of a parasitoid as a biological control agent was also influenced by the relative developmental times of the host and the parasitoid. At 23° C, the mean developmental time of Patasson n. sp. was found to be 11.9 days (Section II). Simonet and Davenport (1981) reported that carrot weevil eggs hatched in an average of 7.1 days at 23.9° C. Using these data in the equation given by Simmonds (1948), the effective parasitism rate computed for the entire observation period (8.5%) would be further reduced to only 5.1%. This reduction is largely the result of the longer time spent inside the host egg by the developing parasitoid. This result suggests that parasitism by Patasson n. sp. represents a relatively minor factor in carrot weevil mortality.

9. Differential Pesticide Effects

Control of carrot weevil infestations by chemical insecticides has been the focus of numerous investigations (Hagmann 1938, Pepper 1942, Wright 1953, Semel 1957, Wright and Decker 1957, Whitcomb 1965, Martel et al. 1975a, Pepper and Ryser 1975, Stevenson 1976a). Pesticide usage is frequently assumed to inhibit the effect of parasitoid populations on their host species. The relative impact of pesticides on Patasson n. sp. and carrot weevil populations must be understood in order to evaluate the role of the parasitoid as an agent of natural control within a commercial agricultural setting. It has been demonstrated that the egg, larval and pupal stages of Patasson n. sp. comprise approximately three-fourths of its total lifespan (Section 4). Thus, most of the parasitoid's life is spent in a relatively insulated environment inside the host egg, which is in turn inside the plant petiole. This may render a degree of protection to the parasitoid population from the effects of pesticide applications. Although the adult population may be severely diminished, a residual population of immatures may remain relatively unaffected.

It was also demonstrated that most parasitoid oviposition occurs within the first few days after the adults have emerged (Section 3). Parasitoids which have survived a particular pesticide application as immatures may be able to emerge and complete most or all of their potential oviposition during the relatively safe interval between applications. This possibility would be enhanced by the use of pesticides which break down quickly in the environment. The objective of this study is to examine the relative effects of several pesticides on the host and parasitoid populations.

9.1 Methods

9.1.1 Study Area

This study was conducted during the 1980 growing season in field #3 at the Hammond Farm in Clinton County, Michigan. This field was planted in onions in 1979, and carrots during 1980. Carrots were planted in four-row beds running north and south. Beds were 1.2 m wide and were separated by ca. 40 cm. The study area consisted of the two beds adjacent to the eastern field margin. The field margin was ca. 12 m wide and consisted of a strip of trees and weeds separating two similar fields. Carrots had been grown in the field to the east of this margin (field #2) in 1979, and the field was planted in beans in 1980. The eastern field was known to have been infested with carrot weevils in 1979, and carrot weevil eggs were parasitized by Patasson n. sp.

Carrots (cv. GT26) were planted in the study field on 3 May, except for the two eastern-most beds. Carrots (cv. Gold King) were planted in the two eastern beds on 9 May.

Fertilizer was applied to this field prior to planting at a rate of 400 lb. per acre. Herbicides were regularly applied to the entire field.

9.1.2 Pesticide Applications

Five chemical insecticides were examined. These included one systemic insecticide (aldicarb) applied in the row with the seed at planting, and four foliar sprays: azinphosmethyl, oxamyl, fenvalerate, and diazinon (Table 13). A randomized block design was used. Each of the three blocks contained eight experimental plots, one for each of the five pesiticides and three control plots. Each plot was 10 m long and two beds wide (ca. 3 m). The entire study area

Table 13. Application dates and rates applied for five chemical insecticides in field number three at the Hammond Farm, Clinton Co., Michigan 1980.

Treatment	Date										
	3 May	13 Jun	23 Jun	30 Jun	7 Jul	14 Jul	21 Jul	4 Aug	11 Aug	18 Aug	25 Aug
Aldicarb (Temik 15G) 1.5 lb ai/A	X										
Oxamyl (Vydate L) 1.0 lb ai/A		X	X	X	X	X	X	X	X	X	X
Fenvalerate (Pydrin 2.4 EC) 0.1 lb ai/A		X	X	X	X	X	X	X	X	X	X
Diazinon (Diazinon AG50) 0.5 lb ai/A		X	X	X	X	X	X	X	X	X	X
Azinphosmethyl (Guthion 2 SC) 1.0 lb ai/A		X		X							

consisted of the southern 240 m of the two eastern beds, divided into 24 contiguous experimental plots. Beginning on 18 June, the northern and southern-most one meter of each experimental plot were kept clear of all vegetation. This was done to prevent pesticide drift or overlap between plots and to inhibit movement of weevils between plots.

9.1.3 Adult Carrot Weevil Trapping

The initial carrot weevil adult population was assessed by trapping adults in the weeds along the eastern field margin. The objective of this procedure was to correlate early spring trap catch data with subsequent field infestation levels. Jar traps baited with carrot baby food were used, as described by Ryser (1975) and modified by Grafius and Otto (1979). Two traps were placed in the weeds adjacent to each experimental plot on 17 May, and were checked on 22 May. The number of adult carrot weevils captured in each trap was recorded, the adults were released at the point of their capture, and then the traps were removed. This trapping was done at about the time of initial carrot plant emergence, which was first observed in the field on 16 May, and in the experimental plots on 21 May. Therefore, the weevil distribution was assumed to be uninfluenced by the carrot plants at the time of this sampling.

9.1.4 Carrot Plant Sampling

Adult carrot weevil activity within the study area was monitored periodically throughout the growing season. This activity was measured indirectly by the examination of host plants. Several plant sampling techniques were used at different times during the growing season, and are outlined below.

Destructive Sampling

The most reliable method of estimating carrot weevil activity is by collecting plants in the field and bringing them into the laboratory for closer examination. However, this technique completely destroys the plants, so that the larger the sample size, the more the processes being estimated are disrupted. The destructive sampling technique was employed on three occasions.

A preliminary sampling was undertaken on 3 June when the carrot plants were just reaching the three-leaf stage. Approximately five plants were collected at one meter intervals from the center of the second row of the marginal bed in each experimental plot. The fresh weight of each plant was recorded and the plants were examined for evidence of carrot weevil activity. The data collected for each plant included the number of feeding or oviposition punctures, the number of egg clutches, and the number of larvae. The number of hatched and unhatched eggs was noted for each clutch. The position of each larva was recorded as in the root or in the foliage. The larval instar was determined for each larva by measuring the head capsule width.

Only plants with eggs (hatched or unhatched) or larvae were included in the analysis. Plants having punctures believed to be made by weevils but which were without eggs or larvae were not considered to be affected by the weevils. These punctures were assumed to be the result of adult feeding which produces no appreciable damage.

Unhatched carrot weevil eggs were extracted from the plant petioles and placed individually in 65 ml clear plastic containers. These eggs were reared in an environmental chamber at a constant 26° C with a 16:8 photoperiod (photophase beginning at 0600 h).

A second set of samples was taken on the day preceding the initial application of the foliar sprays (12 June). The sampling procedure was the same as that described above, except that five plants were collected from each of the eight rows in the experimental plots.

The third set of samples was taken approximately one month after the initial foliar spray applications. Since the outside rows were partially damaged by the sprayer tires, samples (seven plants each) were collected only from the inner six rows of each plot.

Partially Destructive Sampling

An alternative sampling technique was employed on two occasions (3 July and 1 August). These samplings were undertaken to provide additional information concerning parasitism rates while causing a minimum of damage to the carrot plants.

This procedure involved the visual inspection in the field of all plants within one row of each plot. Whenever a stem was located which appeared to have an oviposition hole, it was removed from the plant. No more than one stem was taken from any plant. Thus, the number of stems collected within a plot would be an index of the number of plants showing evidence of carrot weevil activity. The stems were then taken to the laboratory and carrot weevil eggs were extracted. These eggs were reared and information recorded on viability and parasitism.

Final Carrot Weevil Damage Assessment

A final assessment of the extent of weevil activity was made at harvest (13 September). This date was about one month past the time at which weevil

oviposition ended. Therefore, no information concerning parasitism was obtained. All of the plants in the middle six meters of each plot were pulled and the roots were inspected in the field for evidence of damage by carrot weevil larvae. The number of plants with and without apparent weevil damage was recorded. A late season encroachment of weeds into some of the experimental plots produced considerable variation in the number of plants in each plot. In addition, nematode (Meloidogyne hapla) damage, and what appeared to be damage caused by excessive water associated with an unusual amount of fall rain, resulted in a relatively high plant loss. However, damage from causes believed to be unrelated to carrot weevil larvae were not considered in this study.

9.2 Results

9.2.1 Carrot Weevil Infestation

Only 2.1% (3 of 141) of the carrot plants sampled on 3 June had evidence of carrot weevil activity (eggs or larvae). Mean plant fresh weight on this date was 0.10 g (s=0.06). Individual plant weights ranged from 0.01 to 0.34 g. The carrot plants were apparently too small to support a significant carrot weevil infestation at this time.

The mean percent of plants sampled on 12 June which were affected by carrot weevils was 6.6 (Table 14). Significant differences were shown among the treatment means (ANOVA, $p<.005$). The at-planting systemic insecticide (aldicarb) treatment was significantly different from each of the other treatments. No other treatment differences were found. This is consistent with expectations as only aldicarb had been applied by this sampling date. Aldicarb would thus appear to inhibit weevil activities early in the season.

Table 14. Percent of carrot plants with carrot weevil eggs or larvae as affected by insecticide treatment and sampling date.

Treatment	Mean percent of carrot plants with carrot weevil eggs or larvae[ab]		
	12 June	11 July	23 Sept.
Azinphosmethyl	7.4 a	7.8 b	23.6 b
Diazinon	6.6 a	28.3 ab	21.7 b
Aldicarb	Ø.7 b	18.4 b	24.1 b
Oxamyl	6.8 a	14.3 b	12.Ø b
Fenvalerate	3.7 a	16.6 b	13.2 b
Controls	9.2 a	41.9 a	41.5 a

a. Data were transformed by $X' = \arcsin\sqrt{X}$ prior to statistical analysis. The three control plots in each block were considered as subsamples of a single treatment. The significance of differences in treatment means was tested using the pooled sampling and experimental error mean squares divided by the pooled degrees of freedom.

b. In the same column, treatment means followed by the same letter are not significantly different at p=Ø.Ø5, Student-Neuman-Kuel multiple range test.

No relationship was found between the number of adults captured prior to planting in baited jar traps in the weedy area adjacent to the experimental plots and the level of infestation recorded within the associated experimental plots on 12 June (F tests of correlation coefficients, $p>.05$). Relative adult trap catches early in the season thus may not be a useful measure with which to predict the location and severity of subsequent plant damage within the crop site.

The mean percent of plants affected by weevil activity (those with carrot weevil eggs or larvae) in the control treatments among plants sampled on 11 July was significantly different from the means for experimental plots in which azinphosmethyl, oxamyl, fenvalerate, and aldicarb were applied (SNK test, $p<.05$) (Table 14). Thus, these insecticides generally appeared to result in the reduction of weevil oviposition among treated plants.

The mean number of plants encountered on 3 July with carrot weevil eggs (hatched or unhatched) among the stems selected based on a visual inspection of plants while still in the field was significantly lower in the azinphosmethyl treatment than in the controls (SNK test, $p<.005$). However, this sampling failed to detect differences between the control mean and the means in the plots treated with oxamyl, fenvalerate, and aldicarb which were shown by the 11 July destructive sampling. Therefore, the validity of this method can neither be confirmed nor refuted since the results were intermediate between the results of the 12 June and 11 July destructive samplings. However, this method has the advantage of producing less damage to the plants, and requires only a fraction of the time required for a complete examination of the entire plant. This technique may be appropriate for some applications where large areas need to be sampled and time is a critical factor.

The mean number of infested carrot plants in the control plots sampled on 1 August was significantly different than the means of plots treated with fenvalerate and oxamyl (SNK test, $p<.05$). The validity of the partially destructive sampling procedure for estimating damage is questionable on this later sampling date. Only the number of plants encountered which had hatched or unhatched eggs were detected. However, the rate of weevil oviposition is diminished this late in the season. Detection of oviposition is also more difficult on larger plants. The technique overlooked any larvae located inside the plants, which could be expected to represent a large portion of the immature weevil population.

The percent of plants damaged by carrot weevil larvae at harvest differed significantly depending on treatment (Table 14). The control treatment mean was significantly different than all other means (SNK test, $p<.05$). None of the means for plots treated with chemical insecticides were different from one another. All of the chemicals appeared to have inhibited destructive weevil activities, and all appeared to be approximately equal in effectiveness.

9.2.2 Parasitism

Parasitism of carrot weevil eggs by Patasson n. sp. was first detected on 3 June, and continued as long as suitable host eggs were available. No significant differences between parasitism rates in different treatments were found on any sampling date (destructive or non-destructive sampling technique) (ANOVA, $p>.05$). Parasitism rates were thus relatively uniform among treatments, even though carrot weevil egg densities were significantly higher in the control treatments than in some of the plots in which chemical insecticides were applied.

9.3 Discussion

The insecticides examined have been demonstrated to significantly reduce adult carrot weevil activities which bring about economic injury to carrot plants. The systemic insecticide was more effective early in the season. As the season progressed, the foliar treatments were perhaps more effective.

No statistically significant differences were observed between parasitism rates among the various treatments on any sampling date. The percent of weevil eggs parasitized on each date is illustrated in Figure 15, wherein data from the four foliar treatments are pooled.

These results imply that Patasson n. sp. may be able to function sucessfully in a typical commercial agro-ecosystem in which the use of chemical pesticides is prevalent. The protected environment in which the parasitoid undergoes its development and the relatively short life cycle appear to enable the parasitoid to maintain a uniform impact on the carrot weevil population under varying conditions.

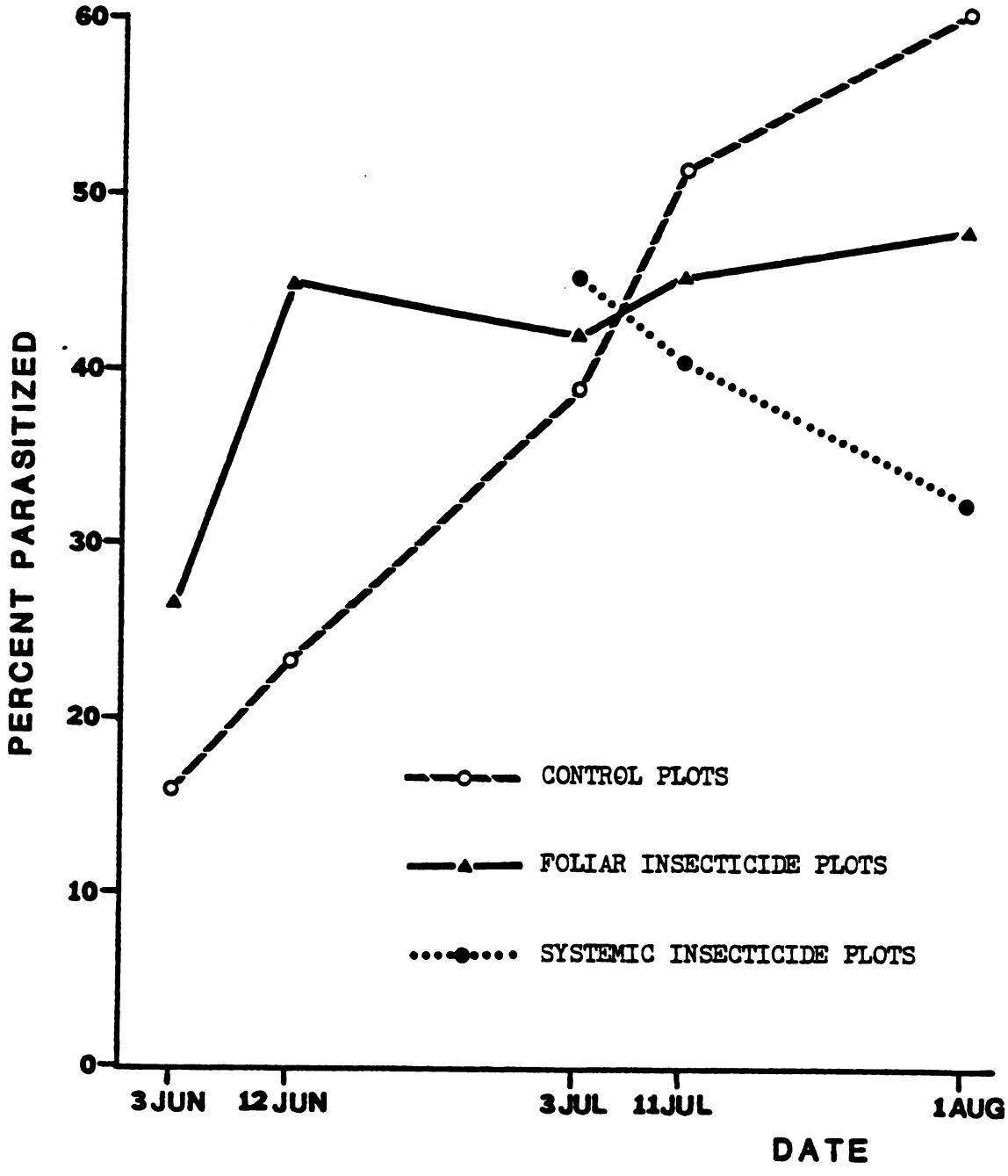

Figure 15. Mean percent of carrot weevil eggs parasitized by Patasson n. sp. in a) plots treated at planting with a systemic insecticide (aldicarb), b) plots treated with foliar applications of insecticides (azinphosmethyl, fenvalerate, diazinon, or oxamyl), and c) untreated controls, Clinton Co., Michigan, 1980.

10. Summary and Conclusions

In 1979, a new mymarid egg parasitoid of the carrot weevil was discovered in a commercial carrot field near East Lansing, Michigan. Identified as Patasson sp. near sordidatus, this parasitoid has since been found at several other locations in Michgan, and in Ohio. Studies were conducted to examine the biology and life cycle of the parasitoid and to evaluate its effectiveness as an agent of biological control. The major findings of these investigations are briefly summarized below.

Up to six parasitoids were found to emerge per field-collected host egg. Most emerged from eggs in which two or three parasitoids developed. The degree of superparasitism was found to affect the size of the adults as well as adult longevity.

Adult longevity was also found to be influenced by temperature. Mean longevity increased from 48.8 h at 29° C to 153.5 h at 17° C. However, this relationship may overstate the effect of temperature on longevity in the field to the extent that the parasitoid is able to change the micro-environmental conditions in which it finds itself by moving from one location to another.

More important than mean longevity is the shape of the survivorship curve. Survivorship was found to be high during the first few days following the emergence of the parasitoid from the host egg. More than 75% of adults kept at 26° C were still alive after three days. After this time mortality increased rapidly. This is important because most parasitoid oviposition is accomplished within a few days of adult emergence regardless of how long the female ultimately lives.

Parasitoid oviposition began within 4-6 h after emergence from the host egg at 23°. More than 50% of all oviposition occurred within two days at 23° C,

although some oviposition occurred up to eight days after adult emergence.

The mean number of offspring per female parasitoid was 49.4. Fecundity was not affected by the number of parasitoids that developed in the host egg from which the female emerged, or by whether or not the female mated. Virgin females produced all male offspring, while mated females produced 77.7% female offspring at 23° C. This method of reproduction provides a built-in mechanism for maintaining a stable sex ratio. This is apparently important to the parasitoid population since there is an additional mechanism by which a stable sex ratio is maintained in the form of a delay in the initiation of oviposition by unmated females of about a day. In the field, such a delay would presumably increase the probability that the female will mate, and thus increase the likelihood of producing female offspring.

Mean parasitoid developmental time was 11.9 days at 23° C. Since about one half of all oviposition occurs within two days after emergence, one complete generation would be completed in about 14 days at this temperature. Therefore, the parasitoid may be able to complete approximately five generations during the period of carrot weevil oviposition.

Developmental time was strongly influenced by temperature. However, while the mean developmental time increased from 9.0 to 17.6 days as temperature decreased from 29 to 17° C, the fraction of the total life cycle spent as immature stages was relatively constant (71.8, 73.4, and 77.4% at 17, 23, and 29° C, respectively). Thus, most of the parasitoid's life cycle is spent in a relatively insulated and stable environment inside the host egg, which is in turn inside the plant petiole. This may provide some degree of protection from external mortality factors such as predation, dessication, and perhaps most

importantly, from the effects of chemical pesticide applications. The impact of several pesticides (fenvalerate, oxamyl, aldicarb, diazinon, and azinphosmethyl) on parasitism was examined in 1980. Parasitism rates were not significantly different in experimental plots treated with the pesticides than in untreated control plots. The parasitoid thus appears to be able to function successfully in a typical commercial agro-ecosystem characterized by frequent pesticide applications.

Emergence periodicity was found to be influenced by both temperature and photoperiod. Most emergence occurred during the first two hours of the photophase from host eggs reared under a photoperiod of LD 16:8. This emergence peak was more pronounced at lower temperatures. Emergence appeared to be controlled entirely by exogenous environmental cues. During the first two hours of the photophase, males appeared to emerge in advance of the females, which may facilitate their location of conspecific females.

Several components of male courtship and mating behavior were identified, including a general excitation phase, a wing fanning display, antennation of the female's abdomen, mounting, and copulation. The females exhibited no overt courtship behavior.

Parasitoid mating readily occurred within two hours of emergence from the host egg. Although this may tend to limit genetic variability within a field population due to an increased likelihood of sibling matings, this disadvantage is apparently compensated for by an increased probability of mating, hence an increased stability of the sex ratio.

Males readily mated more than once in laboratory conditions, but multiple matings by females were not observed. Since female parasitoids were able to

produce female offspring for up to six days after mating, repeated matings by females appear unnecessary.

Carrot weevil and Patasson n. sp. field populations appeared to be spatially synchronous. Parasitism rates were relatively uniform on a given sampling date in different areas of an infested field even though host egg density diminished with distance from the field margin. This suggests that parasitoid dispersal capabilities are adequate to keep pace with movements by the carrot weevil population. This may be important where host and non-host plants are rotated annually, causing a shift in the location of host eggs.

Overwintered carrot weevil adults first became active in the field in April or May, depending on enviromental conditions. In 1980, carrot weevil oviposition was first observed on 9 May on weeds in areas adjacent to a previously infested carrot field. Oviposition on carrots was not observed until 4 June. In 1980, adult parasitoids were active in the field by mid-May but parasitism of carrot weevil eggs was not observed until early June. Once begun, parasitism continued throughout the period of carrot weevil oviposition, which ended in mid-August. Parasitism rates early in the weevil oviposition period were low.

Adult parasitoids remained active in the field as late as 8 November in 1979. This was more than two months after the end of the carrot weevil oviposition period and suggests the possible involvement of an alternative overwintering host.

Carrot weevil larval densities were low in a commercial carrot field studied in 1979. A mean of only 1.46 late instars (third and fourth) was observed per infested plant. Possible mechanisms that could bring about this distribution were examined by manually transferring different numbers of carrot weevil eggs

to uninfested carrot plants and recording larval survival. The survival rate of these weevils was found to decrease as the initial egg density per plant increased. This implies the operation of some density-dependent mortality factor in the field (which is unrelated to parasitism by Patasson n. sp.). Cannibalism has been observed in the laboratory and could account for this density-dependent mortality.

In the field, much of this density-dependent mortality is avoided by an oviposition pattern characterized by low egg densities per plant. Mean clutch size observed in 1979 was 1.99, and the mean number of eggs per carrot plant was 2.87. No density-dependent association was found between host plant density and carrot weevil egg density. Egg density was uninfluenced by plant size. This pattern of oviposition may represent an adaptive strategy which has evolved to efficiently exploit naturally occurring weed host plants. Unlike commercial carrot varieties, these wild host plants have relatively small root systems which are not sufficient to support a large number of larvae. The observed oviposition pattern thus avoids much of the wasted reproductive energy expenditure which would be associated with a larger number of eggs per plant.

The probability that a female parasitoid would find a host egg clutch or a plant with host eggs was uninfluenced by clutch size or the number of eggs per plant. No density-dependent association was found between parasitism rates and host egg density on either a per-plant or per-unit-area basis. Therefore, host searching by Patasson n. sp. appeared to be random.

Among host egg clutches or plants with host eggs in which one or more eggs were parasitized, the percent of eggs parasitized and the number of parasitoids which emerged per host egg were unaffected by either clutch size or

egg density per plant. Therefore, there was a linear relationship between the number of available host eggs and both the number of parasitized eggs and the number of parasitoids produced per plant. Similar relationships were observed on a per-clutch or per-unit-area basis.

In 1979, the nominal parasitism rate (i.e., the overall percent of eggs parasitized) reached a peak of 50.2%. The seasonal mean was 22.8%. However, even in the absence of parasitism, only one or occasionally two carrot weevil larvae per plant successfully complete their development. Therefore, to affect the next generation of carrot weevils, the parasitoid must parasitize all of the eggs on a plant. Since one late instar carrot weevil is sufficient to render a carrot plant unfit for market, all of the eggs on a plant would also have to be parasitized to prevent economic plant damage. Therefore, an effective parasitism rate was defined as the percent of plants on which all available carrot weevil eggs were parasitized. For the observed distribution of eggs per plant, the estimated effective parasitism rate for the 1979 growing season was only 8.5%.

The amount of time spent by the parasitoid in the host egg relative to the time it takes for the host carrot weevil larvae to hatch also affects the interpretation of observed nominal parasitism rates. Using the equation given by Simmonds (1948) that accounts for this relationship, the actual effective parasitism rate was only 5.1% in 1979.

The effect of Patasson n. sp. on carrot weevil populations was examined for two consecutive years in commercial carrot fields with moderate weevil infestations. Observed egg densities per plant were low. Much higher carrot weevil egg densities have been observed in Michigan on infested celery plants (E.

Grafius, Michigan State University, personal communication). Since no density-dependent association between host egg density and the rate of parasitism has been observed, the parasitoid would be even less effective as a control agent at higher egg densities per plant.

Although Patasson n. sp. does not appear to be a major mortality factor affecting carrot weevil populations, it may nonetheless play a more significant role in regulating carrot weevil populations than has been suggested. The findings of the studies presented in this report are based on observations made on crop sites under conditions of high carrot weevil egg densities. Under these conditions, low parasitism rates were observed to occur early in the weevil's oviposition period. A possible explanation to account for these low rates could be that the parasitoid population is limited by the availability of eggs of an alternative overwintering host. However, the carrot weevil is widely distributed at very low population densities among weeds adjacent to field margins. Where the carrot weevil population density is very low, the limiting factor on the parasitoid population may be the scarcity of carrot weevil eggs during the growing season relative to the availability of overwintering host eggs. Therefore, Patasson n. sp. may have a significantly greater role in regulating carrot weevil populations at low densities, and may contribute to the periodic nature of carrot weevil population outbreaks.

An alternative explanation for the low parasitism rates which have been observed to occur early in the carrot weevil's oviposition period could involve an inherent susceptibility to severe abiotic environmental conditions such as cold temperatures. Overwintering conditions may differentially affect the weevil and parasitoid populations, and these effects may vary from year to year. Studies

examining host-parasitoid relationships under a variety of conditions are thus warranted.

Overwintering appears to represent a weak link in the life history of Patasson n. sp. To fully evaluate the role of this parasitoid as an agent of carrot weevil population control, the mode of overwintering must be more completely understood, and is thus a logical focus of future research efforts. In addition, studies examining relationships between Patasson n. sp. and the carrot weevil at low population densities among the weevil's wild host plants could provide information which could ultimately be exploited to enhance the parasitoid's effectiveness through manipulation of conditions outside of the crop site.

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