NOTES ON THE PARASITE COMPLEX OF EVAGORA (RECURVARIA) STARKI FREEMAN IN CANADIAN ROCKY MOUNTAIN PARKS[1]

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Abstract

The known parasites of the lodgepole needle miner, *Evagora* (*Recurvaria*) *starki* Freeman, 27 in all, are listed and notes on the biologies of the most common species are presented. Data are given to show fluctuations in parasite populations from 1944 to 1958. The probable reasons for the ineffectiveness of the parasites to control the needle miner are discussed briefly.

Introduction

The lodgepole needle miner, *Evagora* (*Recurvaria*) *starki* Freeman (6), is a defoliator of lodgepole pine, *Pinus contorta* ssp. *latifolia* (Engelm. ex Wats). It occurred in outbreak numbers in National Parks of Western Canada from about 1936 to 1950 and has been studied intensively since 1948. This paper, the author's fourth and final one in a series based on studies carried out from 1948 to 1959, deals with the species, numbers, and biologies of the parasites of the needle miner. The effect of the parasites on the population dynamics of the needle miner has already been discussed (25).

The Parasite Complex

Table I is a list of the known parasites of *E. starki* as determined by the Systematics Unit, Division of Entomology, Ottawa. The list is compiled from the Annual Reports of the Calgary Laboratory of Forest Biology, the Biological Control Laboratory, Belleville, Ontario, and numerous short publications (7, 9, 14, 20, 21, 22). The order of listing is taken from Muesebeck *et al.* (18).

Copidosoma deceptor Miller, *Apanteles starki* Mason, and *Apanteles californicus* Muesebeck comprise 90% or more of the total number of parasites present in field populations. The remaining species are comparatively rare and little known. Biological notes and comments on abundance are in order of importance.

Notes on Parasite Biologies

Apanteles

Muesebeck (18) states that all species of this genus seem to be internal parasites of lepidopterous larvae. At present, no method has been found to distinguish between the three species of *Apanteles* except in the adult stage. Determination of adults correlated with the sampling and rearing records provides clues to their distribution and abundance. The undetermined species (probably *A. miantonomoi* Viereck) is rare. *A. starki* (13) is the most numerous,

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TABLE I

Parasites of *Recurvaria starki* Freeman

Superfamily	Family	
ICHNEUMONOIDEA	Braconidae	1. *Apanteles californicus* Mues. 2. *A. starki* Mason 3. *A.* sp. poss. *miantonomoi* Vier. 4. *Eubadizon gracile* Prov. 5. *Meteorus pinifolii* Mason 6. *Bracon gelechiae* Ashm.
	Ichneumonidae	7. *Aethecerus pinifolii* Mason 8. *Alegina pinifoliae* (Cush.) 9. *Gelis tenellus* (Say) 10. *Itoplectis obesus* Cush. 11. *Phaedroctonus* sp. near *epinotiae* Cush. 12. *Phaeogenes* sp. near *epinotiae* Cush. 13. *Plectops* n. sp.
CHALCIDOIDEA	Eulophidae	14. *Dicladocerus westwoodii* West. 15. *Derostenus* sp. 16. *Euderus* sp. 17. *Neoderostenus* n. sp. 18. *Sympiesis guttatipennis* Grlt. 19. *Tetrastichus* sp. 20. *Zagrammosoma americanum* Grlt. 21. *Z. nigrolineatum* Cwfd.
	Encyrtidae	22. *Copidosoma deceptor* Miller
	Pteromalidae	23. *Amblymerus* sp. 24. *Habrocytus* sp. 25. *Pachyneuron* sp.
	Chalcididae	26. *Spilochalcis* sp. prob. *albifrons* (Walsh)
SPHECOIDEA	Sphecidae	27. *Passaloecus armeniacae* Ckll.

outnumbering *A. californicus* almost 8:1. *A. californicus* is the most widely distributed, occurring in all sampling locations in the Canadian outbreak including Jasper National Park and on other *Evagora* species in Oregon and California. *A. starki* is apparently restricted to the outbreak in Banff, Yoho, and Kootenay National Parks. The life history notes given probably describe *A. starki* mainly since they are the most abundant and most observations were made on material collected in the Banff area.

Emergence records for 1954 and 1958 show that *Apanteles* emerged in early July at about the same time as the needle miner; parasite emergence in 1956 was markedly earlier and occurred in two peak periods, June 23 and 28. After the first peak of emergence, cold, rainy weather persisted until June 27, the day before the second emergence peak. Emergence continued to about July 7. McLeod (14) recorded emergence of *Apanteles* in late July and August but this did not occur in the field in 1954, 1956, or 1958.

The emergence dates and life spans (about 3 weeks) of *Apanteles* suggest that they parasitize the egg stage of the needle miner. Morgan (17) states that *A. californicus* attacks the egg stage of *E. milleri* in California, but his evidence is also circumstantial.

The parasite is internal and apparently does not affect the normal feeding rate of its host until the latter reaches the fourth or fifth instar (Fig. 1, *a–c*).

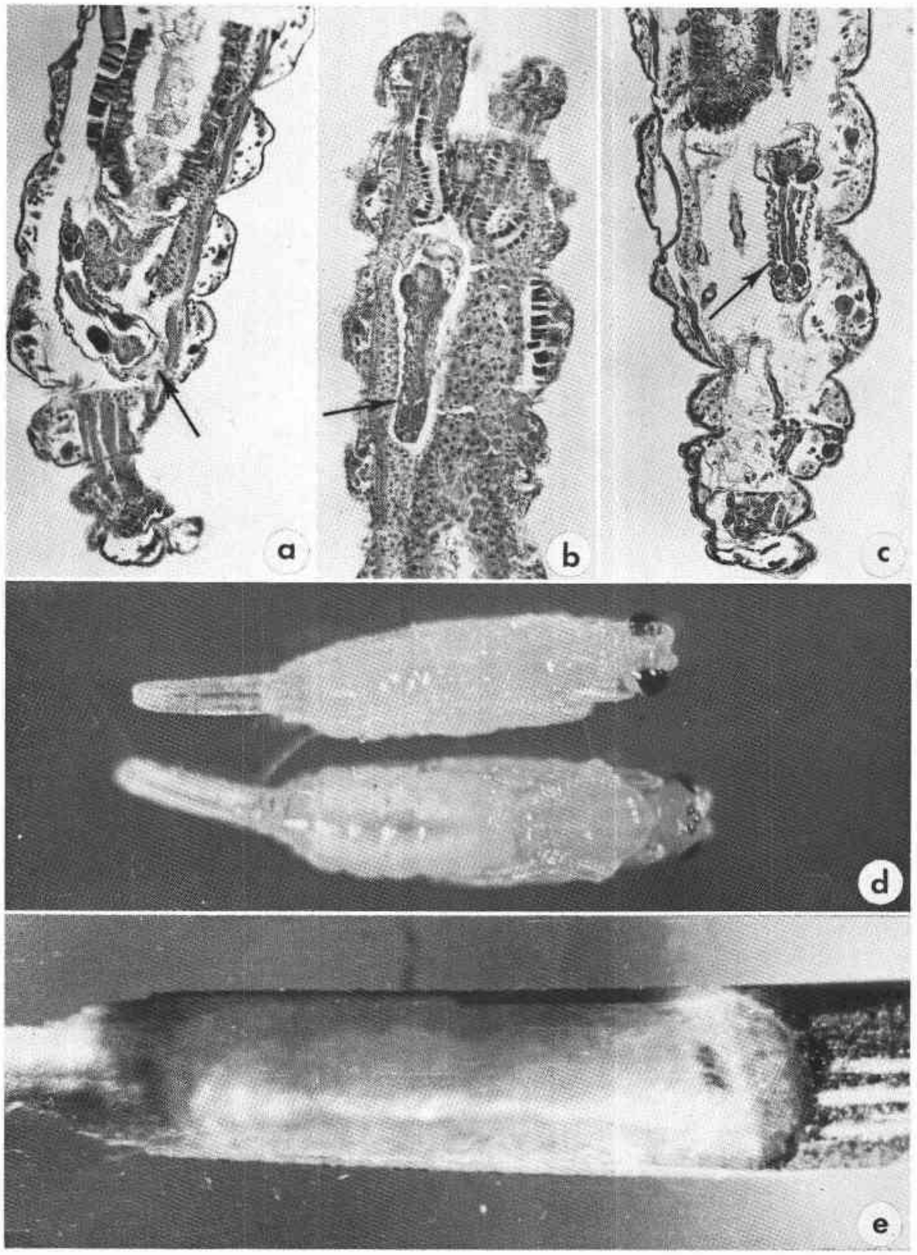

FIG. 1, *a–c*. Photomicrographs of *Apanteles* sp. (probably *starki*) in IV and V instar larvae: (*d*) pupae removed from cocoon; (*e*) cocoon of *Apanteles* sp.

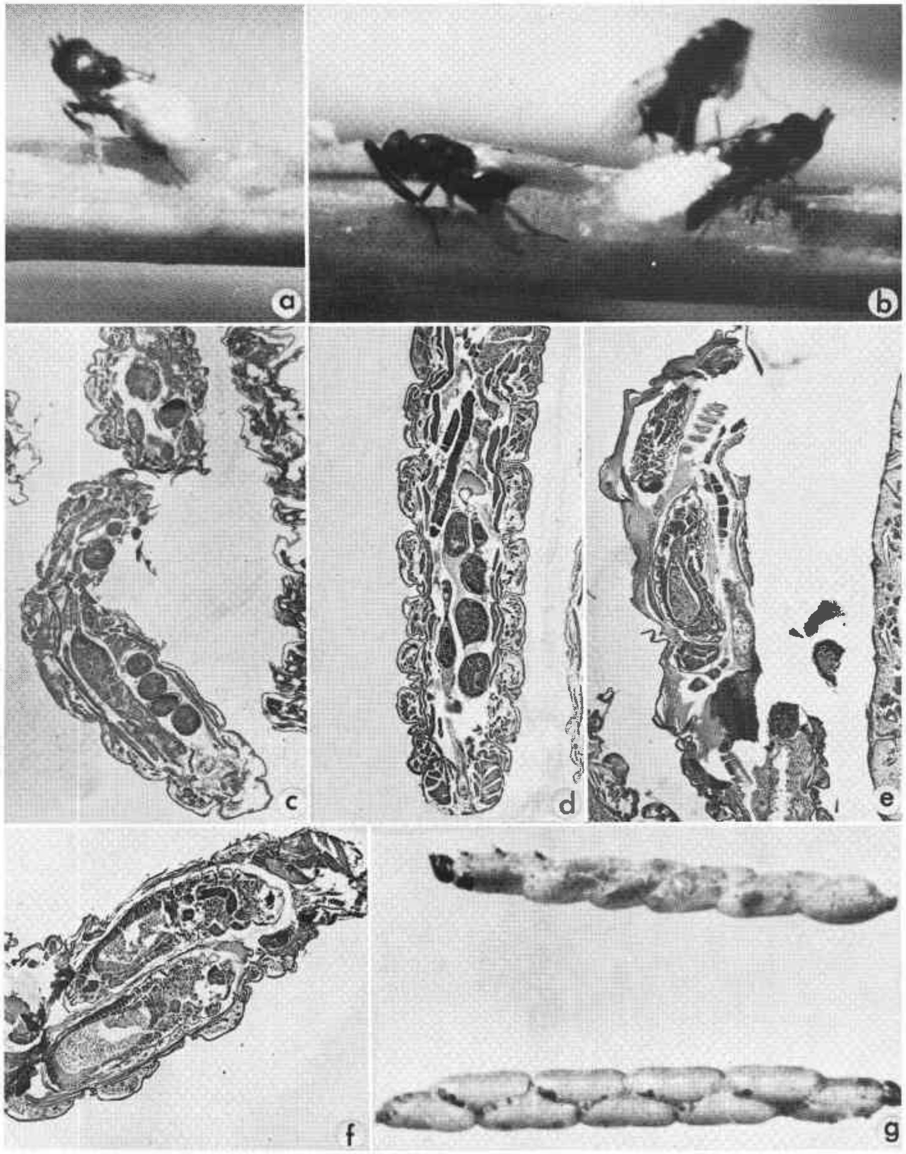

FIG. 2, *a–b*. Adult females of *Copidosoma deceptor* Miller ovipositing in needle miner eggs: e.g., developmental stages of *Copidosoma* in (*c*) III instar, (*d*, *e*) IV instar, and (*f*, *g*) V instar needle miner larva.

Upon the death of the needle miner larva in April or May of the moth flight year, the parasite emerges from the host and spins a white, opaque, silken cocoon within and near the base of the mined needle (Fig. 1, *d*, *e*). This is the first visible evidence of parasitism by *Apanteles.* The emerging adult cuts a circular cap off the cocoon and crawls out of the exit hole prepared by the needle miner larva.

Sex ratios varied from year to year and from location to location but in total averaged almost a 1:1 ratio. There are at least two hyperparasites of *Apanteles*, *Alegina pinifoliae* (Cushman) and *Zagrammosoma nigrolineatum* Crawford. The hyperparasites may be polyembryonic or sometimes deposit more than one egg in the host as *Apanteles* cocoons had up to four emergence holes. The effect of hyperparasitism on *Apanteles* numbers has been negligible.

Copidosoma deceptor Miller

Miller described this species in 1958 and concluded that it was the only *Copidosoma* species attacking *E. starki*, *E. milleri*, and probably other *Evagora* species throughout western North America (16).

It is polyembryonic with as many as 14 adults emerging from a single host larva; the average from *E. starki* was about seven per host. Emergence occurred from July 15 to August 6 in 1954, July 11 to 30 in 1956, and July 5 to 28 in 1958, corresponding with the emergence and oviposition period of the host. There was a marked preponderance of females in some areas but the over-all sex ratio approximated 1:1.

When recently emerged adult females were placed in vials with mined needles containing host eggs they determined the location of eggs by tapping the needle with their antennae. If an egg cluster was beyond its reach from the exit hole, the adult female would either abandon the needle or search for some alternative access to the egg cluster. Several adults were seen to oviposit in the same eggs when placed in a vial with only one egg cluster. Individual females were seen ovipositing into the same egg several times (Fig. 2, *a*, *b*).

It is presumed that the development is similar to that described for *C. gelechiae* Howard (11). Early developmental stages of the parasite were not found in larval sections until the third instar of the needle miner (Fig. 2, *c*) and following this were easily recognizable in the fourth (Fig. 2, *d*, *e*) and fifth (Fig. 2, *f*) instars. As the needle miner does not reach the third instar until the second year of larval development, it is possible that the parasite overwinters in the polygerm stage, development progressing rapidly throughout the summer of the larval stages of the host. The parasites do not kill the host until it is in the fourth or fifth instar and do not become visible externally until the host is dead (Fig. 2, *g*).

Eubadizon gracile Provancher

Little is known of the subfamily (Blacinae) to which this parasite belongs. *E. gracile* is listed from New Brunswick to British Columbia in Canada, and Maine and California in the United States. Other hosts are *E. milleri*, *Recurvaria piceaella* Kearfott, *Dioryctria reniculella* (Grote), *Choristoneura fumiferana* (Clemens), *Archips* sp. (18), and the black-headed budworm, *Acleris variana* (Fernald) (Prebble, pers. comm.). It was widely distributed throughout the outbreak area in small numbers but occasionally became locally abundant.

The parasite is internal and leaves the carcass of the fourth or fifth instar larva in late May of the moth flight year. It spins a tough, brown, translucent cocoon within the needle midway between the base of the mine and the exit hole. The needle miner larva is unaffected until early May. Parasite emergence has occurred as early as June 18 and as late as July 10. Specimens in captivity lived only a few weeks.

Sympiesis sp.

McLeod (14) reported this as an external parasite of needle miner larvae, relatively abundant in Alberta prior to 1951. The sampling program from 1948 to 1958 showed that it was scarce. Parasites believed to be *Sympiesis* sp. have been recovered from needle miner larvae and pupae and also from the important parasite, *Copidosoma deceptor* Miller. A *Sympiesis* sp. is recorded as an external parasite on late instar larvae of *E. milleri* (17, 26).

Zagrammosoma americanum Girault

This was one of the parasites recorded earliest from Alberta. It was found emerging from needle miner larvae and also from cocoons of *Copidosoma deceptor*. Since that time it has regularly appeared in mass rearings but in small numbers. Recent collections contained a second species, *Z. nigrolineatum* Crawford, which is parasitic on *Apanteles* spp. as well as needle miner. Two species of *Zagrammosoma* are recorded from California, *Z. americanum* and a new (?) species (17, 26).

Phaeogenes sp.

Members of the subfamily to which this species belongs (Cryptinae) have been described as internal parasites of Lepidoptera that oviposit into either the host larva or pupa, but always emerge from the pupa (18). The only note made on this rare species is that it was observed emerging from the needle miner pupa on August 4 and was extremely active. Depending on the length of adult life it could parasitize either needle miner eggs, first instar larvae, or an alternate host. There was some evidence to suggest that it may have a 1-year cycle.

Neoderostenus n. sp.

Neoderostenus n. sp. was reported as an important parasite by McLeod in 1951 (14) but sampling since that time indicates that it, as well as the other two eulophids, is relatively rare. It completes its development in the host pupa and may parasitize the larva in the same year, carrying over on alternate hosts. It forms the naked black pupa typical of eulophids. There are usually four to six parasites per pupa but whether this is due to polyembryony or superparasitism is not certain. It is also recorded as a parasite of *Copidosoma* species (14).

Notes on Parasite Population Fluctuations

Prior to 1948, estimates of parasitism were based on a limited number of samples (7, 8). The first reasonably accurate estimates were made in 1948 and for the succeeding two needle miner generations. Precise estimates, with a better understanding of the species involved, were made in 1954, 1956, and 1958.

Percentage of parasitism for all areas is presented in Table II and for specific areas in subsequent tables (Tables III and IV). The estimates in these tables are based upon the populations present just prior to the winter before the moth flight year and indicate only the percentage of parasites which reached maturity. Although the effective parasitism with relation to the surviving host population would have been more meaningful, the earlier data were not gathered in a manner which would permit this. Table II shows the trend of parasitism over the period of the outbreak. The life tables presented later are a basis for demonstrating effective parasitism in future studies. Two values are shown for the spring of 1950. Twelve per cent was calculated on the basis of the number of parasites visible in the spring. However, many of these were dead, presumably as a result of winter kill. The percentage surviving (i.e. emerging), and thus the percentage of parasitism, obtained from mass rearing material collected in the spring was 1.7%.

TABLE II

Percentage parasitism in moth flight years (all areas)

Year	Parasitism, %	Most important parasite species (in numbers)
1944	11	*Copidosoma deceptor* Miller
1946	10	—
1948	10	—
1950	12 to 1.7	*Copidosoma deceptor* Miller
1952	10	*Copidosoma deceptor* Miller
1954	18	*Copidosoma deceptor* Miller *Apanteles starki* Mason *Apanteles californicus* Mues.
1956	30	*Apanteles starki* Mason *Copidosoma deceptor* Miller *Apanteles californicus* Mues.
1958	21	*Apanteles starki* Mason *Copidosoma deceptor* Miller *Eubadizon gracile* (Prov.) *Apanteles californicus* Mues.

TABLE III

Percentage parasitism in moth flight years for four areas now under constant investigation

Area	1950	1952	1954	1956	1958
Mount Eisenhower	19–3.7	4+	20	39	25
Bankhead	11–1.9	17	16		
Girouard				32	29
Massive	13–0	—	10	26	15
Cathedral	0	22	14	12	15

Partial records are available for several areas which demonstrate the variability of parasitism within the general outbreak area. These are summarized for areas selected to correspond with the four areas now being continuously studied (Table III). Two estimates are given for the 1950 samples in this table also.

The distribution of the principal parasites by location and elevation in 1954 is of interest (Table IV). These data clearly show the importance of three of the parasite species. Although its occurrence is not wholly consistent throughout the outbreak area, *Apanteles* appears to be more numerous in the valley bottom than on the slopes. This suggests that this species is more cold-hardy than *Copidosoma deceptor*, or that there is a fundamental difference in conditions required for oviposition.

Supplementary tables for the critical spring period of the moth flight year for the four areas on a continuous study basis are presented in Tables V to VIII, which relate to Tables I to VIII in Stark, 1959 (25). It was demonstrated that when the parasite population was estimated on the same sample unit as the needle miner (number per branch tip) their numbers remained more or less

TABLE IV

Species composition and parasitism in all areas sampled in 1954

			By species, % of total parasitism		
Location	Elev.	Parasitism*	*Copidosoma deceptor*	*Apanteles starki* and *californicus*	Others
Mount Eisenhower	4800	—	—	—	—
	5300	1.1	39.0	59.0	2.0
	5800	3.2	86.0	13.5	0.5
	6300	3.7	83.0	16.5	0.5
Massive	4800	0.1	—	100.0	—
	5300	1.5	47.4	52.6	—
	5800	5.9	48.4	51.6	—
	6300	2.3	21.0	79.0	—
Cathedral	4500	—	—	—	—
	5000	1.1	53.9	45.1	1.0
	5500	3.1	40.4	58.6	1.0
Lake Louise	5000	—	—	—	—
	5500	0.8	81.0	18.5	0.5
	6000	0.3	95.3	4.2	0.5
	6500	0.1	92.6	3.6	3.8
Brewster Creek	5200	7.0	37.9	61.9	0.2
Baker Creek	6000	9.2	30.8	69.2	0
Cascade Valley	5500	3.9	60.0	39.7	0.3
Saskatchewan Crossing	4700	0.2	11.3	88.7	—
Hawk Creek	4000	1.2	83.4	16.6	—

*Number of parasites per 5-year branch tip; the sampling unit used for the lodgepole needle miner (Stark 1958 (23)).

constant throughout the period of the outbreak (25, Fig. 9). Absolute parasite numbers actually increased following the high needle miner mortality year (1949–50) but have decreased steadily since 1954 (Table IX). However, as the percentage parasitism generally increased (Table III) this decline must have been at a slower rate than that of the needle miner population.

Discussion

It is generally accepted that population growth follows a logistic curve where density increases until a point is reached at which the trend will be reversed and the rate of increase begins to decline. It is also generally assumed that this reversal is brought about in two ways: through new and more severely unfavorable processes coming into play at successively higher levels of density and by

TABLE V

Supplementary life tables showing mortality of late instar larvae and pupae, Mount Eisenhower*

x	1*x*	*d*×*F*	*dx*	100*qx*
		1954–56		
Instars III–IV (1955–1956)	416	Climate—winter mortality	143	34.37
Instars IV–V	273	Parasitism		
		Copidosoma deceptor Miller	86	31.50
		Apanteles starki Mason *Apanteles californicus* Mues.	68	24.90
		Eubadizon gracile (Prov.)	5	1.83
		Undetermined species	1	0.38
			160	58.61
		Unknown	8	2.93
			168	61.54
Pupae	105	Unknown—poss. climate	26	24.76
		Parasitism		
		Phaeogenes sp. and others Less than	1	0.45
			26+	25.21
		1956–58		
X_3, X_4—III and IV instar, July, 1957	261	Various	27	10.34
X_5—IV and V instar	234	*Copidosoma deceptor* Miller	40	17.09
		Apanteles starki Mason *A. californicus* Mues.	51	21.79
		Eubadizon gracile (Prov.)	0.5	0.21
		Unknown spp.	3.5	1.50
			95	40.59
X_6—Pupa and adults	139	*Phaeogenes* sp.	8	3.42

*Table headings: *x*, stage at which sample is taken; 1*x*, the number surviving at the beginning of the stage noted in the *x* column; *d*×*F*, the mortality factor responsible for *dx*, the number dying within the interval between successive samples; 100*qx*, percentage mortality.

an increase in the intensity of action of various individual density-dependent factors or processes (19). From the data presented it can be seen that the parasites of the needle miner did not conform to this population theory nor could any of the population damping mechanisms discussed by Klomp (10) be demonstrated as effective in this study.

It is postulated that the climatic effects which permitted the "release" of the needle miner population in the period 1936 to 1950 (25) did not benefit the parasite population to the same extent. The first effect considered was that the parasites suffered heavier mortality during the winters of the outbreak but at low needle miner populations the evidence suggests the opposite to be true. That is, the parasite population is decreasing at a slower rate than the needle miner. Clausen (2) recognized, particularly with introduced parasites, that differential mortality of parasites can be a limiting factor to parasite success. These species may not be able to withstand as low temperatures as their hosts. Dowden's work (5) is an outstanding example of these effects.

TABLE VI

Supplementary life tables showing mortality of late instar larvae and pupae, Massive Mountain

x	1*x*	*d*×*F*	*dx*	100*qx*
		1954–56		
III–IV instars	465	Various	96	20.65
IV–V instars, May, June, 1956	369	Predation by birds	124	33.60
		Parasitism		
		Apanteles starki Mason *Apanteles californicus* Mues.	66	17.89
		Copidosoma deceptor Miller	52	14.09
		Eubadizon gracile (Grov.)	3	0.81
		Undetermined species	2	0.54
			123	33.33
			247	66.94
Pupae June, 1956	122	Climate—desiccation?	30	24.84
Emerged	92			
		1956–58		
X_3, X_4—III and IV instar, July, 1957	151	Various	89	58.94
X_5—IV and V instar	62	*Copidosoma deceptor* Miller	13	20.97
		Apanteles starki Mason *A. californicus* Mues.	13	20.97
		Eubadizon gracile (Prov.)	2	3.23
		Unknown spp.	1	1.61
			29	46.77
X_6—Pupa and adults	33	No parasitism		

Control of the oyster-shell scale by *Aphytis mytilaspidis* is usually effective in the mild-wintered Annapolis valley in Nova Scotia but is ineffective in New Brunswick where winter temperatures fall to −20° F or lower (12). The success of parasites of scale insects in California is limited by low temperatures and extreme temperature fluctuations in the winter (3, 4). Uvarov (28) reviews several studies which show a differential mortality of parasites at low temperatures. Some internal parasites are more sensitive to low temperatures than the host in which they exist. However, he also gives examples which show that low temperatures can favor parasite populations where the parasitized hosts are less susceptible to temperature extremes than non-parasitized ones. Blais *et al.* (1) found this to be true for parasites of the forest tent caterpillar. Unseasonably warm weather in May followed by several days of freezing temperatures caused high mortality of larvae but its principal parasite was unaffected.

A second limitation to parasite success is thought to be the differential effect of weather on developmental rates. Uvarov (28) gives ample evidence to show that host and parasite are very often unequally adjusted to normal climatic

TABLE VII

Supplementary life table showing mortality of late instar larvae and pupae, Mount Girouard

x	1*x*	*d*×*F*	*dx*	100*qx*
		1954–56		
III–IV instars	896	Various	228	25.44
IV–V instars, May–June, 1956	668	Predation by birds	76	11.38
		Parasitism		
		Apanteles starki Mason *A. californicus* Mues.	228	34.13
		Copidosoma deceptor Miller	50	7.48
		Undetermined species	10	1.50
			288	43.11
		Unknown	41	6.14
			405	60.63
Pupae June, 1956	263	Climate—desiccation	56	21.29
		Parasitism—unidentified species	2	7.60
			58	28.89
Emerged	205			
		1956–58		
X_3, X_4—III and IV instar, July, 1957	219	Various	15	6.85
X_5—IV and V instar	204	*Apanteles starki* Mason *A. californicus* Mues.	82	40.20
		Copidosoma deceptor Miller	22	10.78
		Eubadizon gracile (Prov.)	6	2.94
		Unknown spp.	1	0.49
			111	54.41
X_6—Pupa and adults	93	No parasitism		

conditions and will react to disturbances in different ways. Slight differences in rate of development may have a profound effect on the success of a parasite, particularly when the stage attacked is of short duration and the period of oviposition of the parasite is equally short. Thus, DeBach *et al.* (4) found that winter temperatures affected the rate of development of the parasite of a scale insect and disrupted the synchronization of parasite emergence with the stage attacked, resulting in markedly reduced parasitism. It has been shown above that the emergence dates of two of the major parasite species of the needle miner were markedly different in two different generations. If the assumption

TABLE VIII

Supplementary life table showing mortality of late instar larvae and pupae, Cathedral Mountain

x	1*x*	*d*×*F*	*dx*	100*qx*
		1954–56		
III–IV instars	181	Various	117	64.64
IV–V instar, May–June, 1956	64	Parasitism		
		Apanteles starki Mason *A. californicus* Mues.	17	25.56
		Copidosoma deceptor Miller	4	6.25
		Undetermined species	1	1.56
			22	24.37
Pupae				
June, 1956	42			
Emerged	42			
		1956–58		
X_3, X_4—III and IV instar, July, 1957	30	Various	5	16.67
X_5—IV and V instar	25	*Eubadizon gracile* (Prov.)	7.8	31.20
		Apanteles starki Mason *A. californicus* Mues.	1.0	4.0
		Copidosoma deceptor Miller	0.6	2.4
		Unknown spp.	0.6	2.4
			10	40.0
X_6—Pupa and adults		No parasitism		

TABLE IX

Number of parasites per branch tip in moth flight years

Year	Mount Eisenhower	Bankhead–Girouard*	Massive	Cathedral
1950	3.3	0.30	—	—
1952	0.85	—	—	—
1954	2.36	3.84	6.7	1.4
1956	1.60	2.90	1.23	0.22
1958	0.95	1.11	0.29	0.1

*The sample location was changed from Bankhead to Girouard in 1956.

is correct that these species are parasites of the egg stage, then the numbers of these species would be expected to be less in 1958 and this proved to be the case in some areas.

Another possible factor, based solely on example and speculation, is that cold temperatures may reduce the fecundity and fertility of the parasite to a greater degree than its host. There is ample evidence to indicate that fecundity and fertility of insects are affected by external factors. This study has dealt largely with winter extremes but these effects may occur at any time during the life cycle (28). DeBach *et al.* found that the fecundity of a parasite of the California red scale was markedly reduced by detrimental effects of winter weather (4).

Thalenhorst (26) states that in nature, parasites and predators rarely attain their theoretical maximum efficiency and gives as a major reason for this that the hosts are rarely dispersed uniformly over an area, even under outbreak conditions. Differences in mobility and the 'searching ability' of the parasite may place the parasite at a distinct disadvantage. Environmental conditions during adult parasite activity may seriously limit their ability to search out the habitat of the stage attacked by them. So many variables are involved in determining the success of parasitism in comparison to that of the host that it is not surprising that parasites may be ineffective in controlling populations of the host insect.

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